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REVISION OF THE MARSUPIAL GENUS *PLANIGALE* TROUGHTON (DASYURIDAE)

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ABSTRACT

Planigale Troughton, 1928 is revised and a new generic diagnosis provided. Five species are recognized: *P. ingrami* (Thomas, 1906) (including the forms *subtilissima* Lönnberg, 1913, and *brunnea* Troughton, 1928); *P. tenuirostris* Troughton, 1928; *P. gilesi* Aitken, 1972; *P. maculata* (Gould, 1851) (formerly regarded as a species of *Antechinus* Macleay, 1841 and including the form *Phascogale minutissima sinualis* Thomas, 1926); and *P. novaeguineae* Tate and Archbold, 1941. These species are placed in three groups: the *P. maculata* group, the *P. ingrami* group, and the *P. gilesi* group. *P. gilesi* is regarded as the most specialized species, having completely lost the last upper and lower premolar. Two additional forms of *Planigale* noted, one from northwestern Western Australia and another described by Lundelius and Turnbull (1973), may represent additional species.

The genus *Planigale* is considered to be related to *Ningaui* Archer, 1975 as well as to some *Antechinus*-like dasyurids such as *Phascogale* Teminck, 1824. There is also some affinity with *Sminthopsis* Thomas, 1888, but the common features that some species of these two genera share may be the result of convergence in arid adaptation.

In 1928 Troughton proposed that *Phascogale subtilissima* Lönnberg and *P. ingrami* Thomas should be included with *Planigale tenuirostris* Troughton in the genus *Planigale*. Subsequently, *Planigale novaeguineae* Tate and Archbold and *Planigale gilesi* Aitken were described. The placement of *maculatus* Gould in *Antechinus* by most modern authors (e.g. Tate 1947, Ride 1970) is anomalous. Archer (1975) considers it to be within *Planigale*.

Some non-*Planigale* species (in *Antechinus*) exhibit characters previously believed confined to *Planigale*—in particular, flatheadedness (Ride 1970)—while inclusion of *P. novaeguineae* and *P. gilesi* in *Planigale* indicates that not all *Planigale* are minute in size. Minute dasyurids are now known to occur in another dasyurid genus, *Ningaui* Archer. These developments in classification and taxonomy emphasize the need for revision in the genus *Planigale*.

METHODS

Cranial measurements are given in Table 1. The method of taking measurements is shown in Figure 1. Characters of particular importance in differentiating species of *Planigale* are nasal lengths, widths, contact between premaxillae and nasals, distance between posterior lacerate foramen and anterior edge of alisphenoid bulla (or tympanic wing), transverse distance across foramen magnum, and skull depth in front of alisphenoid bullae. Similarly, external measurements were made of the ear (from notch to tip of pinna), supratragus (maximum length), nose–vent (anus), tail–vent, and hind foot (less claws). Unless otherwise noted, measurements were made on preserved materials from which skulls had already been removed. External measurements should not be considered directly comparable with measurements of fresh material (e.g. Lidicker and Marlow 1970).

Some small dasyurids have distinctive morphological dental and cranial characteristics. Within genera, such as *Sminthopsis*, these characteristics are sufficiently constant to diagnose species. In other genera, such as *Planigale*, these distinctive morphological characters are less common. Only *Planigale gilesi* in lacking P4 is obviously and consistently distinct from other species. Recognition of other species of *Planigale* requires examination of size and consideration of relative cranial and dental proportions. A statistical summary of absolute size in species of *Planigale* is given in Table 1. A summary of cranial, dental, and external proportions, as ratios, is given in Table 2.

These ratios are as follows:

1. Basicranial length/zygomatic width (BL/ZW): an estimate of brachycephaly;
2. Minimum inter-orbital width/ZW (IO/ZW): an estimate of relative mid-cranial frontal restriction;
3. Alisphenoid bullae width (left and right combined)/ZW (BW/ZW): an estimate of relative width of alisphenoid bullae;
4. BW/M^{1-3}: an estimate of alisphenoid bullae width relative to M^{1-3} length;
5. Bullar length (measured from posterior lacerate foramen to anterior edge of expanded alisphenoid bulla/M^{1-3} (BL/M^{1-3}): an estimate of relative length of periotic and alisphenoid bullae (or tympanic wing) inflations;
6. Skull depth (measured vertically immediately anterior to alisphenoid bullae)/ZW (SD/ZW): an estimate of relative depth of skull;
7. SD/BL: an estimate of skull depth relative to skull length;
8. SD/(C^1 – M^4): an estimate of skull depth relative to length of cheek-tooth row;
9. SD/IO: an estimate of skull depth relative to mid-cranial restriction;
10. Foramen magnum diameter (maximum transverse)/SD (FM/SD): an estimate of relative size of foramen magnum;
11. M^{1-3}/ZW: an estimate of width of skull relative to M^{1-3} length;
12. (C^1 – M^4) — (M^1 – M^4)/(M^{1-3}) (=C^1 – P^4/M^{1-3} in Table 2): an estimate of length of (C^1 – P^4) relative to M^{1-3} length which is also an estimate of relative cheek-tooth row crowding;
13. (I_1 – M_4) — (M_{1-4})/(M_{1-3}) (=I_1 – P_4/M_{1-3} in Table 2): an estimate similar to 12 above, but for lower teeth and involving lower incisors;
14. Nasal length (maximum)/BL (NL/BL): an estimate of relative length of nasals;
15. Nasal width (maximum across both nasals)/ZW (NW/ZW): an estimate of relative width of nasals;
16. NW/NL: an estimate of relative length and width of nasals;
17. Premaxillary–nasal suture/NL (PN/NL): an estimate of relative length of premaxillary-nasal suture;
18. Minimum distance between premaxillary and maxillary vacuities/BL (VV/BL): an estimate of relative palatal evacuation;
19. Dentary length (from posterior edge articular condyle to anterior edge of I_1 alveolus)/BL (DL/BL): an estimate of relative length of dentary;
20. Tail-vent length/head–body length (TV/HB): an estimate of relative length of tail;
21. Hind foot length/HB (HF/HB): an estimate of relative length of foot;
22. Length of supratragus of ear/ear height from notch (ST/E): an estimate of supratragus length relative to ear height.

These ratios were selected following an overall examination of specimens which indicated that although there were apparent differences in cranial structure, expression of some of these was confused by differences in relative size. As a result, ratios were computed using absolute measurements for each specimen. Means of these ratios were then obtained.

Cranial, dental and external terminology is that used by Archer (1975, 1976). Abbreviations for specimen numbers unless otherwise indicated are as follows: AMNH, American Museum of Natural History; BM, British Museum (Natural History); C, National Museum of Victoria; D, Victorian Fisheries and Wildlife Department; JM or J, Queensland Museum; B, Butler collection in the Western Australian Museum; 67.8.73, example of number in fossil collection, Western Australian Museum; NTM, Northern Territory Museum. The following institutions all have M as a prefix to their mammal specimens. To distinguish them, a prefix indicating the institution has been added to the number as follows: AM M——, Australian Museum; SAM M——, South Australian Museum; WAM M——, Western Australian Museum.

Family DASYURIDAE

Genus **Planigale** Troughton

Planigale Troughton, 1928, p. 282.

TYPE SPECIES: *Planigale ingrami brunneus* Troughton, 1928, by original designation. (Not *P. ingrami* Thomas, 1906, as cited by Tate 1947, and Laurie and Hill 1954).

DIAGNOSIS

Dasyurids smaller than *Antechinus*, and differ from these in having extremely reduced maxillary vacuity; very small paracone on M^{1-3} and small talonids on M_{1-3}. Differ from *Sminthopsis* and *Antechinomys* Krefft, 1867 in possessing straight uncurled external edge on supratragus of ear; short, broad pentadactyl hind foot; enlarged metatarsal granules; nasals broadened posteriorly; apparent lack of squamoso-frontal contact on external surface of skull; posterior cingula present M^{1-3}; reduced protocone and paracone on M^{1-3}; reduced talonid on M_{1-3}; P_4 single-rooted or absent; palatine vacuity lacking. Differ from *Ningaui* in possessing very broad hind foot: straight uncurled external edge of supratragus of ear; posterior cingula on M^{1-3}; nasals markedly broadened posteriorly; no palatine vacuities.

Description

Tail thin without brush or crest and approximately equal to, or longer than, nose–vent length.

Supratragus of ear with straight external edge. Helix curls beneath root of supratragus. Anterior edge of tragus bears short hairs. Up to two fold lines for retraction of pinna. Notch on posterior edge of pinna variably present.

Mysticial vibrissae on each side in 6–7 ill-defined rows with 2–6 vibrissae in each row; 1–3 supra-orbital vibrissae; 6–8 genal vibrissae; 3–4 carpal vibrissae.

Hindfoot broad with 7 post-digital pads including 3 interdigital, 1 hallucal, 1 post-hallucal, 1 anterior and 1 posterior outer metatarsal pad. All pads with apical granules appearing transversely striated, although striae do not normally exist as physical ridges on surface of granules. Sole naked except near heel. Hallux clawless.

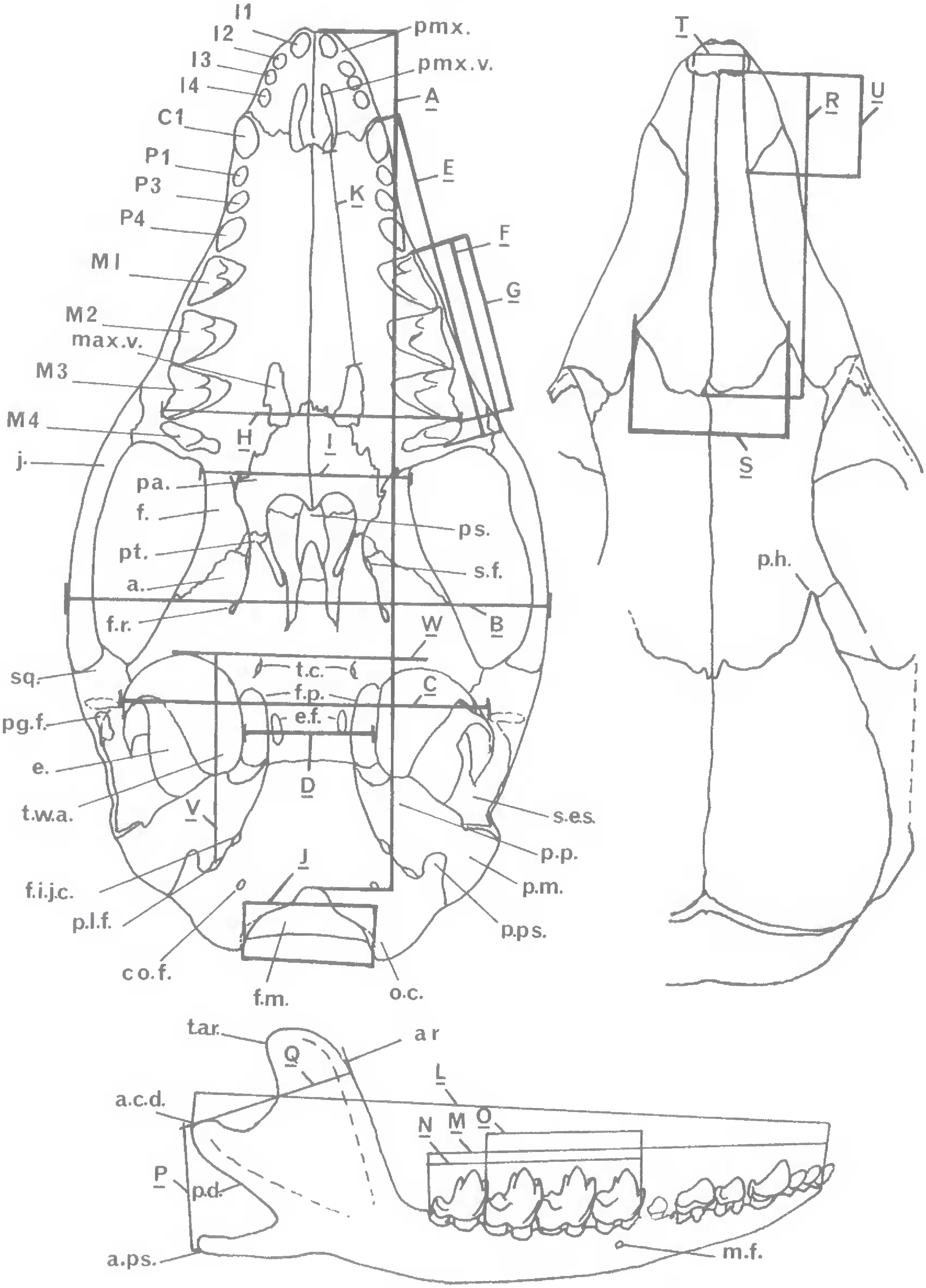
Pelage generally lacks distinctive markings. Abnormal variation includes spots.

Median groove pronounced and to top of rhinarium. Groove demarcating whole of external rim of rhinarium. Nostrils centrally situated on each side.

Five to twelve nipples have been noted in this study. Fleay (1967) records fifteen juveniles attached to one female *P. maculata* (as *P. ingrami*).

Nasals broadly widened posteriorly. Premaxillary-nasal contact shorter than maxillary-nasal contact. Lacrimal foramen on rim of orbit or just anterior to it. Infra-orbital foramen opens onto surface of maxilla without contact with jugal. Postorbital process on frontal absent. Prominent venous foramen in frontal on dorsal rim of orbit. Contact between squamosal and frontal apparently lacking on outside of skull. Variably developed, anterior, dorso-lateral extensions (horns) of squamosal and parietal present. Postero-mesial edge of palatine at point of contact with frontal in orbit extremely variable in shape. Cranium flattening reasonably constant intraspecifically but various interspecifically. Premaxillary vacuity short, not extending posteriorly beyond posterior edge of canine alveolus. Maxillary vacuity very short not exceeding length of premaxillary vacuity. Palatine vacuity lacking. Postero-lateral palatal vacuity lacking or so incomplete as to be barely suggested. Posterior palatal spine generally not well-developed. Pterygoid with spinous hamular process. Alisphenoid tympanic wing poorly developed with short periotic contact. Periotic with low, variably enlarged tympanic wing. Ectotympanic large with only small portion covered by alisphenoid tympanic wing. Transverse canal of basisphenoid very small to absent (or indistinguishable) from anterior end of foramen pseudovale. Variably developed entocarotid canal adjacent to elongate narrow foramen pseudovale. Opening of eustachian canal large. Internal jugular canal enclosed in tube formed by basioccipital and periotic. Tiny posterior lacerate foramina variable in number and antero-mesial to paroccipital process. Condylar foramina tiny to large and variable in number (includes hypoglossal foramen). Paroccipital process barely inflated as continuation of anterior tympanic wing of periotic. Stapes columnar, but generally (perhaps universally) with very tiny stapedial depression near contact of foot plate with columella. Depth of dentary ventral to teeth variable. Masseteric fossa wide. Mandibular foramen beneath M_1 or M_2.

I^1 largest incisor and separated from I^{2-4} by diastema. I^{2-4} incisor crown length and height variable but I^3 generally highest. C^1 tallest crown in upper dentition. Base of C^1 enamel crown often far above alveolar rim with tiny posterior cuspule and barely distinguishable to absent buccal and lingual cingula. P^4, when present, largest upper premolar. P^1 never larger than, but sometimes subequal to, P^3. Small posterior cuspule on P^{1-4} sometimes absent. Cingulum around P^{1-4} generally entire. Paracone very reduced and close to metacone of M^{1-3}. Paracone increases in height from M^{1-4}. Basal antero-posterior length of protocone decreases from M^{1-4}. Tiny protoconule variably present on M^{1-3}. No metaconule on M^{1-4}. Preprotocrista continuous with anterior cingulum, which is complete on M^{1-4}. Postprotocrista continuous with posterior cingulum on M^{1-3} which extends buccally for approximately two-thirds posterior length of each molar. Prefossa tilts postero-buccally and not enclosed posteriorly except by posterior cingulum of M^{1-3}. Metacone absent on M^4. Paracrista of M^1 variably reduced to absent. Paracrista of M^{1-4} increases in length posteriorly. Metacrista of M^2 never shorter than metacrista of M^1 and M^3. Stylar cusp A not clearly distinguishable on any molar, possibly homologous with part of antero-buccal cingulum of M^1. Stylar cusp B of M^1 often completely indistinguishable and may be totally reduced or fused with paracone. Stylar cusp B, as defined by buccal edge of paracrista, present on M^{2-4} but largest in M^{2-3}. Stylar cusp C tiny, only variably present on posterior flank of stylar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cusp B or anterior flank of stylar cusp D of M^{2-3}. Stylar cusp D large on M^{1-2}, tiny on M^3. Stylar cusp E tiny to absent on M^{1-3}. Generally, where stylar cusps C and E tiny to absent, buccal fossae of each molar tilt buccally and are not enclosed on either side of stylar cusp D. Ectoflexus greatest in M^3 and decreases anteriorly. Buccal length of M^{1-4} decreases posteriorly. Anterior width of M^{1-3} increases posteriorly with M^4 anterior width never greater than that of M^3. I_1 crown taller and longer than I_2. I_2 taller and longer of subequal to I_3. Small posterior cingular cusp on C_1 – P_4 variably developed or absent. Buccal and lingual cingula developed on C_1 – P_3 not generally complete at anterior edge. Development of cingula on P_4 varies with size of tooth. C_1 widest antemolar tooth. P_4 varies from absent to peg-shaped to oval. When P_4 present, generally single-rooted but rarely double-rooted. Protoconid considerably largest trigonid cusp of M_{1-4}. Metaconid height of M_{1-3} exceeds paraconid, but smaller or subequal to paraconid of M_4. Difference between paraconid and metaconid decreases posteriorly in M_{1-3}. Middle of protoconid posterior to middle of buccal side of trigonid root. Hypoconid decreases in height posteriorly in M_{1-4} being absent or miniscule on M_4. Entoconids tiny to absent on M_{1-4} but when present most noticeable on M_2. Variable tiny to absent parastylid on buccal opening of trigonid. Variable tiny to absent metastylid on postero-buccal edge of metaconid. Conspicuous anterior cingulum on M_{1-4} but may be only partly developed on M_1. Lingual confluence of posterior cingulum and posterior hypocristid defines hypoconulid. Prominent hypoconulid notch in anterior cingula of M_{2-4}. Well-developed carnassial notch between protoconid-paraconid and protoconid-metaconid but, generally, carnassial groove very tiny to absent. Talonid wider than trigonid of M_1, narrower or subequal to trigonid of M_2, and progressively narrower than trigonid of M_{3-4}. Paracristid M_3 longer or subequal to that of M_2 which is longer than paracristid of M_4 which is longer than paracristid of M_1. Metacristid of M_{2-3} subequal and larger than paracristid of M_4 which is larger than that of M_1. Posterior hypocristid of M_2 longer than that of M_1 and subequal to that of M_3.

Generic Discussion

Troughton's (1928) concept of *Planigale* is based on the relatively flat-headed forms, *P. tenuirostris* and the *subtilissima* and *brunnea* forms of *P. ingrami*. As a result, he considers flat-headedness an important characteristic of the genus. Although *P. maculata* and *P. novaeguineae* have relatively less-flattened skulls, other dental and cranial characters are the same as in other species of *Planigale* and quite unlike any other dasyurid genus. Thus flat-headedness is not maintained as constant in *Planigale*. Flat-headedness probably enables the individual to squeeze into narrow crevices as suggested by Troughton (1967), Walker (1967) and others, and permits use of the head as an efficient wedge to raise objects, such as stones or bark, covering insects. Many dasyurids, including *P. maculata* and the *subtilissima* form of *P. ingrami*, studied in captivity use their heads for this purpose. Some *Antechinus* are also flat-headed (Ride 1970, Archer and Calaby in preparation), indicating that this adaptation has developed in more than one dasyurid lineage.

Species of *Planigale* generally lack an external squamosal-frontal contact. Exceptions are presumably abnormal. For example, in a specimen of *P. gilesi* (AM M7393) the left side of the skull shows clear exclusion of a squamosal-frontal contact, while the right squamosal may just contact the frontal. The bones are semi-transparent rendering identification of sutures difficult, and internal suture relationships may be apparent on the outside. These bones overlap rather than directly

Fig. 1: Terminology and mensuration in the skull and dentary of *Planigale* (based on *P. maculata*). *a.*, alisphenoid; *a.c.d.*, articular condyle of dentary; *a.ps.*, angular process; *ar*, anterior border of ascending ramus; *co.f.*, condylar (and/or hypoglossal) foramen; *e.*, ectotympanic; *e.f.*, entocarotid foramen; *f.*, frontal; *f.i.j.c.*, foramen for internal jugular canal; *f.m.*, foramen magnum; *f.p.*, foramen pseudovale; *f.r.*, foramen rotundum; *j.*, jugal; *max.v.*, maxillary vacuity; *m.f.*, mental foramen; *o.c.*, occipital condyle; *pa.*, palatine; *p.d.*, posterior border of dentary; *pg.f.*, postglenoid foramen; *p.h.*, parietal horn; *p.l.f.*, posterior lacerate foramen; *p.m.*, mastoid part of periotic; *pmx.*, premaxilla; *pmx.v.*, premaxillary vacuity; *p.p.*, petrosal part of periotic; *p.ps.*, paroccipital process; *ps.*, presphenoid; *pt.*, pterygoid; *s.e.s.*, squamosal epitympanic sinus; *s.f.*, sphenorbital fissure; *sq.*, squamosal; *t.a.r.*, tip of ascending ramus; *t.c.*, transverse canal; *t.w.a.*, tympanic wing of alisphenoid; *A–V*, positions from which cranial measurements were made: *A*, basicranial length; *B*, maximum zygomatic width; *C*, outside bullar distance; *D*, inside bullar distance; *E*, C^1–M^4; *F*, M^{1-4}; *G*, M^{1-3}; *H*, LM^3–RM^3; *I*, interorbital width; *J*, maximum width of foramen magnum; *K*, interpalatal vacuity distance; *L*, dentary length; *M*, I_1–M_4; *N*, M_{1-4}; *O*, M_{1-3}; *P*, tip of angular process to articular condyle; *Q*, articular condyle to anterior border of ascending ramus; *R*, maximum nasal length; *S*, maximum nasal width; *T*, minimum nasal width; *U*, nasal-premaxillary suture length; *V*, bullar length; *W*, line to which V is measured and represents antero-most level of alisphenoid tympanic wing.

abut, so that while they may not contact outside the skull, they may do so inside. A similar situation occurs in WAM M2846, a specimen of the *subtilissima* form of *P. ingrami*, where both sides are in doubt.

All generic characters given as diagnostic are separately shared with at least one other dasyurid genus, and no single character can be considered unequivocably diagnostic of *Planigale*. As with *Ningaui* (Archer 1975), it is to be expected that distribution among other dasyurids of characters found in *Planigale* will in part reveal intra-familiar relationships.

It has been suggested that *Planigale* is a derivative of an *Antechinus*-like dasyurid (e.g. Troughton 1967, Ride 1970). The narrow molars, non-transversely orientated hypocristids, lack of palatine vacuities, wide nasals, apparent lack of squamosal-frontal contact on the outside of the cranium, wide feet, and short ears, are characters of *Antechinus*-like dasyurids such as *Phascogale*, but are not characters of the genus *Sminthopsis*. *Ningaui* provides a structural link between *Planigale* and *Sminthopsis*. This link is further suggested by *S. ooldea*, which exhibits mild paracone and talonid reduction, features well-developed and characteristic of *Ningaui* and *Planigale*. In general, species of *Planigale* appear most similar to *Ningaui*, *Antechinus*, and *Phascogale*, but also distantly similar to *Sminthopsis*. Direct similarity to *Sminthopsis* is minimal and involves characters which may be arid-adaptations achieved independently in *Sminthopsis* and *Planigale*.

Development of widespread arid habitats in Australia may have resulted in independent development of arid-adapted characters in several *Sminthopsis* and *Antechinus* species groups and in other dasyurids such as *Dasycercus* Peters, 1875 and *Dasyurides* Spencer, 1896. Some presumably arid-adapted characters are small body size, relatively short premolar rows, high-crowned teeth, dolichocephaly, and well-fenestrated palates. All except the last two are characteristic of *Planigale*, and some species such as *P. tenuirostris* are dolichocephalic.

The **Planigale maculata** group

This group comprises two species, *P. maculata* Gould and *P. novaeguineae* Tate and Archbold.

Planigale maculata (Gould)
(Plates 43, 44, 51C–D)

Antechinus maculatus Gould, 1851, letterpress to pl. 44.
Antechinus minutissimus Gould, 1852, letterpress to pl. 45.
Phascogale minutissima sinualis Thomas, 1926, p. 634.
Planigale maculata Archer, 1975, p. 248.

Types

Antechinus maculatus Gould, 1851

Holotype: BM53.10.22.21, skin and skull, adult male, collected by J. Strange. The holotype has not been examined.

Type Locality: Gould (1851, letterpress to plate 44) says '. . . was procured in the brushes near the river Clarence, a little to the southward of Moreton Bay.' Gould (1854, p. 284) says 'Brushes of the River Clarence, on the east coast of Australia.' Thomas (1888, p. 293) records the locality as 'Clarence R., Moreton Bay . . .'. Tate (1947, p. 131) says the type specimen came '. . . from Clarence River, south of Moreton Bay, southern Queensland . . .'.

Antechinus minutissimus Gould, 1852

Holotype: BM53.10.22.20, skin and BM54.10.21.5, skull, adult male, collected by J. Strange. The holotype has not been examined.

Type Locality: Gould (1852, letterpress to plate 45) says '. . . habitat of the *A. minutissimus* is the districts on the eastern coast of Australia, in the neighbourhood of Moreton Bay.' Gould (1854, p. 285) says 'Hab. Brushes of the east coasts of Australia.' Thomas (1888, p. 293) gives 'Cressbrook, Moreton Bay . . .'.

Phascogale minutissima sinualis Thomas, 1926

Holotype: BM26.3.11.194, skull and carcase in alcohol, juvenile male, obtained by Captain G. H. Wilkin's Expedition, 19 January 1925. The holotype has not been examined.

Type Locality: Thomas (1926, p. 634) says 'Hab. Groote Eylandt, Gulf of Carpentaria.'

Material Examined

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Mapoon Mission (AM M8149); Abergowrie (JM833); Coen (AM M8150); Wenlock (J8170); Mt Molloy (e.g. J16477); Mt Garnet (J7766); Herberton (J8244); East Funnell Creek above Sarina (AM M6983); Sarina (AM M6840); Yeppoon Crossing, Rockhampton (AM M8336); Rockhampton (J19668); Mt Larcom (J7002); Calliope (J8070); Biloela (J9856); Biggenden (J4374); Saunders Beach Rd, N. Townsville (Qd Museum); Upper Ross Store, Townsville (JM826); Major Creek, Woodstock (JM823); Lansdowne Stn, Woodstock (Qd Museum); Collinsville (WAM M6203); Coorgango Stn, nr Proserpine (J20256); Russell I, Moreton Bay (J10826); West Burleigh (J13171); Tamborine (J16685); Purga (e.g. J4105); Upper Brookfield, Brisbane (J13396); Maryborough (AM M662); Coogan Range, nr Yarraman (J13272); Aurukun Mission (e.g. C1483); Adel's Grove, Lawn Hill Ck (AM M5636).

New South Wales: 8 km W. Ballina (AM M8338); Bunnan, nr Scone (AM M7555); Boomi Creek, Urbenville (CSIRO no. CM492); Wallaby Knob, Tooloom (CSIRO no. CM233).

Northern Territory: Fogg Dam, Humpty Doo (e.g. WAM M8095); Darwin; Mataranka Homestead (AM M7382); King River (C7820); Katherine (AM M7043); Jim Jim Ck (W.A. Museum).

Western Australia: Drysdale River (W.A. Museum); Barrow Island (WAM M11020).

Distribution of specimens shown in Fig. 2.

Diagnosis

Large species similar in size to *P. gilesi*, but differs from *P. gilesi* in possessing three premolars above and below and having non-reduced stylar cusp B. Differs from *P. novaeguineae* in smaller mean size and in several cranial ratios including higher BW/ZW and BW/M^{1-3} which reflect relatively larger size of alisphenoid bullae. Differs from *P. ingrami* in being larger with non-flattened skull; larger M^2 stylar cusp D; relatively shorter supratragus of ear; greatly enlarged P^4, almost twice P^1 crown height; non-reduced stylar cusp B; relatively conspicuous transverse canal foramen; paritals with relatively shorter, antero-dorsal extensions (horns); small condylar foramen; and several cranial ratios including large mean SD/IO and PMX-NE/NL and smaller mean BL/M^{1-3}, FM/SD, and NW/NL. Differs from smaller *P. tenuirostris* in possessing relatively conspicuous transverse canal foramina, larger M^3 stylar cusp D, shorter head, and in lower BL/ZW ratio.

Fig. 2: Distribution of *Planigale maculata* (solid squares represent modern specimens examined; solid triangles represent literature records given by Marlow 1958 and Thomas 1926), and *P. gilesi* (solid dots represent modern specimens examined).

Description

Tail thin. Tail length variable being shorter than head-body length in typical form, longer in *sinualis* form, and, in general, relatively shorter than in other species. Davies (1960) lists external measurements for specimens of *sinualis* form from Humpty Doo, N.T. (as *P. ingrami*), which indicate mean TV/HB value of 0·90. This compares closely with series from Groote Eylandt described by Johnson (1964) with mean TV/HB value of 0·93. Type specimen of *sinualis* Thomas has TV/HB value of 0·90. Compared with this, typical *P. maculata* here examined have mean TV/HB value of 0·82.

Supratragus of ear longer in typical form than *sinualis* form, and relatively shorter than in most other species.

Nipple number varies from 5 to 10 (to possibly 15, Fleay 1967) in typical form, and 8 to 12 in *sinualis* form. Thomas (1888) records 8, Pocock (1926) records 6, Fleay (1965) records 7–9 (as *P. ingrami*, here regarded as including *P. maculata*, see below), for typical form and notes (1967) specimen with 15 young. In specimens of typical form examined here, two had 5 nipples (J21325, J8244), two had 6 (AM M6840, J2204), one had 7 (AM M662), one had 8 (J3345) and three had 10 (J21321, J19668, and J4374). From single locality, Mt Molloy, NE. Qd, J21325 had 5, and J21321 had 10. Davies (1960) records litters of 8 and 12 for animals from Humpty Doo, N.T., representing *sinualis* form. Aslin (1975) notes litters of 8, 10 and 11 for wild caught Humpty Doo animals. Johnson (1964) records 10 nipples for single specimen of *sinualis* form from Groote Eylandt. Specimen from Darwin has 10 nipples.

Pouch morphology varies in typical form, perhaps as function of reproductive stage. Juveniles held in captivity and examined live (5 August 1973) had poorly-developed, inconspicuous pouch. Adults, including live mother of juveniles noted above, had well-developed, deep pouch, but size and position of opening vary. Live adults appear to have ability to contract entrance to small, posteriorly positioned, circle. One individual examined (5 August 1973) had well-developed pouch which opened posteriorly, with walls on sides and 10 mm deep wall at anterior end. Some preserved adults (e.g. J21321 from Mt Molloy), apparently lactating, have pouches widely open postero-ventrally, presumably to accommodate larger young. Woolley (1974) comments on pouch morphology in *P. maculata*.

Mean IO/ZW ratio lower than in most other species, reflecting relatively restricted interorbital regions. Mean FM/ZW, and NW/NL ratios lower than in most other species. Mean (C^1–M^4)–(M^{1-4})/(M^{1-3}) lower in typical than *sinualis* form and, in general, lower than in most other species. Mean SD/IO ratio higher in typical than *sinualis* form, reflecting less-flattened condition of typical skulls, and higher in this ratio than all other species except *P. novaeguineae*.

Discussion

Although the holotypes of *Antechinus maculatus*, *Antechinus minutissimus* and *Phascogale minutissimus sinualis* have not been examined, topotypical material of *maculatus* and *minutissimus* has been examined. Consideration of this material, type descriptions, and descriptions given by Thomas (1888), Tate (1947), and Johnson (1964) leaves no doubt about the synonomy presented here. No topotypical specimens of *sinualis* have been examined. Few cranial measurements are given by Thomas (1926) and Johnson (1964) for *sinualis* but, where given, they closely correspond to measurements for Humpty Doo *Planigale* specimens.

Fleay (1965) records *P. ingrami* from Gin Gin, Gunalda, Numinbah Valley and Burleigh in SE.Qd. These records are apparently unsupported by museum specimens of *P. ingrami*. Several specimens (e.g. J13526 and J13171) collected by Mr Fleay from owl pellets at Burleigh, represent *P. maculata*. Fleay (1965) also reports *P. ingrami* from Monto, SE.Qd. The only museum specimen from Monto in the Queensland Museum (J15783) appears to represent *P. tenuirostris*. It is possible that the animals studied by Fleay may have represented both *P. maculata* and *P. tenuirostris*, although photographs, nipple counts and measurements given suggest only *P. maculata*.

Ride (1970) reports *P. maculata* from Western Australia. The specimen regarded by Ride (pers. comm.) to be *P. maculata* (WAM M3432) from Tambrey, Coolawanyah Station, may represent an undescribed taxon, and is discussed below (p. 357).

In general, *P. ingrami* and *P. maculata* are allopatric. The only instance of apparent sympatry between them occurs at Major Creek, Woodstock, NE.Qd (*P. maculata* JM823 and *P. ingrami* JM764). Marlow (1962) suggests they are also sympatric at Coen, NE.Qd. Examination of this material (AM M8148 and AM M8150) suggests both specimens represent *P. maculata*.

Specimens referred to *Planigale* by Van Deusen (1969) from northern Australia have not been examined. If *P. ingrami* occurs in areas of the Northern Territory other than the Barkly Tableland, it should be easy to distinguish this extremely flat-headed, tiny species from *P. maculata*.

Forms of *P. maculata:* There are at least two distinctive, allopatric forms of *P. maculata*. The typical form includes samples from Mt Molloy, Townsville, and other localities in eastern Queensland and northeastern New South Wales generally in and east of the Great Divide. A non-typical form occurs in northern Northern Territory, northwestern Queensland, Barrow Island and the Drysdale River area of Western Australia. No attempt has been made here to assess the possible statistical basis for recognizing subspecies. This non-typical form includes the type of *Phascogale minutissima sinualis* Thomas and the name *sinualis* is used here only as a convenient means of reference. This use is not to be interpreted as formal recognition of subspecific status. At present, too little information is available about *Planigale* from Cape York to determine the affinities of specimens from Aurukun Mission. They differ in several respects from *sinualis* and may represent a third form. Measurements of spirit carcases provide a mean TV/HB value of 0·77, the lowest for any *maculata* series measured here. Shorter tails are recorded by other workers. Fleay (1965) reports two inch tails and three inch head and body measurements for male *P. maculata* (as *P. ingrami*) which gives a TV/HB ratio of 0·67. The mean ST/E value of the Aurukun Mission animals is very low and compares only with the mean figure for *P. tenuirostris*. Absolute size of almost all characters is smaller in Aurukun Mission specimens than in any other *maculata* measured. The only Aurukun female with a distinct pouch area appears to have nine very small nipples. It was evidently collected in August.

Although it is concluded here that the types of *maculatus* Gould and *sinualis* Thomas are conspecific, it is clear that they also represent different forms. The only major geographic barrier which appears to separate the allopatric ranges of these forms is the Gulf of Carpentaria. The Aurukun Mission population from the eastern edge of the Gulf of Carpentaria may be unique as a result of its isolation from the typical form by the inland areas of the Cape York Peninsula and from the *sinualis* form by the Gulf. It is probable that during the Plesitocene, with lowered sea levels, the Gulf of Carpentaria was not a significant barrier.

Habit and Reproduction

Typical *maculata:* In N.S.W. they are rare and inhabit sclerophyll and rain-forest on the eastern side of the Great Divide (Marlow 1958). In Qd they are recorded from hollow logs and under sheets of iron, in timber country, flooded marsh, and rocky areas (Fleay 1965); most specimens brought to the Queensland Museum from Brisbane area have been killed by cats; one was collected from a Cane Toad's stomach (Covacevich and Archer 1975).

In captivity they sometimes build saucer-shaped nests of dry grass or in deeper grass, more elaborate nests similar to those of Blue Wrens (Fleay 1965). Animals held by the author seemed opportunistic, building nests in hollow logs, between sheets of newspaper, and in boxes. As many as five individuals may nest together. Food preferred is insects but eggs, lean meat, chicken and honey are accepted. Small lizards and mammals are avoided. Movements in captivity indicate they are adept climbers, not hesitating to jump or drop distances of over 30 cm.

Fleay suggests from field observations and breeding in captivity that individuals of the typical form are summer breeders, earliest pouch development and pregnancy taking place in October and, if no pregnancy occurs, the pouch stops development by mid-January. Captive animals from Mt Molloy held by the author mated on 11 September 1973. This resulted in birth, but actual date of birth was not noted.

Sinualis form: At Humpty Doo, N.T., they occupy *Pandanus* and *Melaleuca* fringe areas bordering the Adelaide River flood plain (Davies 1960). In W.A. one individual was collected in hummock grass beneath *Acacia* on sandstone boulders in sand, on the edge of a tributary of the Drysdale River (Dr D. Kitchener, pers. comm.).

Aslin (1975) gives breeding data for this form in captivity, noting that it is polyoestrous with a gestation period of 19–20 days. Litters were born in February, March, April, July, September, October and December, single females having two or possibly more litters per year. Males were capable of breeding at least to 24 months in age. These observations are supported by the combined observations of Thomas (1926), Davies (1960), and Johnson (1964) which suggest this form is also polyoestrous in the field.

Planigale novaeguineae Tate and Archbold (Plate 45)

Planigale novaeguineae Tate and Archbold, 1941, pp. 7–8.

Type

Holotype: AMNH108561, skull and skin, adult male, collected by G. H. H. Tate, 20 January 1937. The holotype has not been examined.

Type Locality: Tate and Archbold (1941, pp. 7–8) state: '. . . Rona Falls, near Port Moresby, Central Division, Papua: 250 metres . . .'.

Material Examined

Data sheets are available in the library of the Queensland Museum.

New Guinea: ♂, Waigani Swamp 16 km N. Port Moresby, coll. H. Cogger, 23 December 1963 (AM M9091); ♀, New Guinea, no other data (J4368).

Diagnosis

Similar to *P. maculata* but differs in larger size; tendency for I^4 to exceed I^2 in crown length; several dental and cranial ratios including lower mean BW/ZW, BW/M^{1-3}, FM/SD, and higher mean SD/ZW and I_1–P_4/M_{1-3}; and in variable tendency for tail to be longer than head and body. Differs from other species of *Planigale* by same features which distinguish *P. maculata*.

Description

Tail length variable, shorter than head and body in holotype and specimens noted by Ziegler (1972) but longer than head and body in J4368.

Hind foot, from description by Tate and Archbold (1941, p. 8), dried in holotype with 'Faint traces of striations on pads (rest of foot normally granulated as in *Antechinus* and other genera)'.

Nipple number unknown.

Mean BW/ZW and BW/M^{1-3} values lowest in *Planigale* reflecting very small alisphenoid bullae of *P. novaeguineae*. Mean SD/ZW value highest reflecting relatively deep skull of *P. novaeguineae*. Mean FM/SD value lowest indicating both narrow foramen magnum and relatively deep cranium. Mean (I_1–M_4)–(M_{1-4})/M_{1-3} value highest.

Discussion

The type specimen was previously the only specimen of *Planigale* recorded from New Guinea. Ziegler (1972) records three additional specimens, from Balimo, 450 km WNW. of the type locality. Two additional specimens were collected at Waigani Swamp, 16 km N. of Port Moresby, New Guinea, by Dr H. Cogger of the Australian Museum in 1963. Mr B. Marlow of the Australian Museum will describe these specimens elsewhere, but in the meantime has kindly allowed me to examine the skull of the adult male specimen, AM M9091. Menzies (1972) records numerous specimens of this species obtained from owl pellet material collected from the floor of a rock shelter near Mt Eriama, about 16 km from Port Moresby and 13 km from Rouna. A specimen in the Queensland Museum (J4368) identified on the label by Mr C. W. De Vis as coming from New Guinea, represents *Planigale*. The specimen is represented by a skull, dentaries and dry, shrivelled and faded, carcase. A manuscript in De Vis' handwriting states that the fur is '. . . short and silky throughout . . . mammae not apparent . . . pads smooth of the three at the bases of the digits and the outermost has a small backward-curved prolongation; the plantar pad on the hallucal side elongate and semi-divided, that on the outer side opposite and shorter . . . above dark fawn, sides of muzzle distinctly darker but without a definite stripe; edges of eyelids nearly black, chin and throat nearly white passing into pale fawn on the rest of the lower surface, feet and tail brown above, paler brown below . . . length of head and body 69 mm . . .'. He expresses all other body measurements as percentages of the head-body length. Converting these values, the tail is 70·4 mm, the hind foot length (possibly including claws) 13·8 mm, hind foot breadth 3·0 mm, the ear (it is not apparent how it was measured and the figure seems small) 6.2 mm, the forearm and manus 11·0 mm. The habitat is stated to be 'New Guinea, locality unrecorded'.

Differences between J4368, and AM M9091 from Waigani Swamp, include the greater skull depth of AM M9091, 6·3, compared with 5·6 for J4368, indicating an SD/IO value of 1·34 for AM M9091 and 1·12 for J4368. Other differences are minor by comparison, and it is likely that these are sexual, AM M9091 being a male and J4368 a female. In other series, such as those of *P. maculata*, males almost invariably have deeper skulls and narrower interorbital values than females. Tate and Archbold's (1941) description of the type of *P. novaeguineae* indicates that although the skull was damaged in preparation, the braincase was, in their opinion, very flat. This specimen is a male, and therefore the degree of flattening may vary within, as well as between, sexes. Ziegler (1972) notes other possible sexual differences in *P. novaeguineae* from Balimo.

J4368 is smaller in many cranial and dental measurements than AM M9091. Measurements given by Tate and Archbold (1941) for the holotype are generally intermediate between these two. J4368 indicates that there is not as great a size difference between *P. novaeguineae* and other *Planigale* as the type specimen alone suggests. For example, AM M6893, male *P. maculata* from East Funnell Creek above Sarina, Queensland, is in most characters only just smaller than J4368 and in BL, ZW, OBW, R–LM^3, VV, C–AP, and PLF–AB even exceeds J4368. Further, in some specimens (e.g. AM M6983 and AM M8336) of *P. maculata*, I^4 slightly exceeds I^2 in length, as in *P. novaeguineae*.

Tate and Archbold (1941, p. 8) describe the hind foot of the holotype as having 'Faint traces of striations . . .' on the pads. Tate (1947, p. 134) says of this specimen that it is '. . . the only one in which the foot pads are distinctly striated'. In alcohol specimens of *P. maculata* examined in the present study, most apical granules of the interdigital hallucal and metatarsal pads have visible striae without surface ridges. In some (e.g. C7428) the covering skin is thin on the apical granules and very low ridges appear present on the surface of the pad. In some alcholic specimens of other species (e.g. AM M5021 *P. ingrami*) the apical granules are also striate with extremely low ridges on the pads. It has been noted in *Sminthopsis* (Archer, in preparation) that dehydration may emphasize striations by causing shrinkage of tissues over underlying sub-surface ridges. It is possible that the difference in opinion about the striate condition of the type specimen of *P. novaeguineae* given by Tate and Archbold (1941) and Tate (1947) may be the result of seven years of dehydration. In any case, the fact that other species sometimes have striated apical granules indicates that *P. novaeguineae* is not unique in this respect. It may, however, be a more common feature of specimens of that species.

Habitat and Reproduction

The type specimen (Tate and Archbold 1941, p. 8) was caught on a '. . . great rock-strewn slope . . . in a dryish place beneath an overhanging rock. The hillside was comparatively barren of vegetation . . .'. Ziegler (1972) notes that specimens caught at Balimo occurred in 'grass'. Menzies (1972, p. 404) notes that with the possible exception of a doubtfully identified juvenile *Pseudocheirus*, all of the species occurring with *P. novaeguineae* in the owl pellet material from near Port Moresby '. . . are savanna dwellers. Closed forest lies within a few miles of the site and so well within the hunting range of a medium–sized bird but it is clear that it hunts only in the savanna.' He suggests that the relative abundance (6·5%) of the dasyurid material (over 90% of which was *Planigale*), may represent the abundance of these animals in the small mammal fauna of the Port Moresby savannas.

The **Planigale ingrami** group

This group comprises two species, *P. ingrami* (Thomas) and *P. tenuirostris* Troughton.

Planigale ingrami (Thomas)
(Plates 46, 47, 51 A–B)

Phascogale ingrami Thomas, 1960a, pp. 541–2.
Phascogale subtilissima Lönnberg, 1913, pp. 9–10.
Planigale ingrami brunneus Troughton, 1928, pp. 282–5.

Types

Phascogale ingrami Thomas, 1906a

Holotype: BM6.3.9.77, skull and skin, adult male, collected by Mr W. Stalker, 30 April 1905. The holotype has not been examined.

Type Locality: Thomas (1906b, p. 541–2) states 'Buchanan, Alexandria, 600′ . . . central part of Northern South Australia'.

Phascogale subtilissima Lönnberg, 1913.

Holotype: Stockholm Museum no. 2482, skull and mounted skin, juvenile male, collected by the Swedish Scientific Expeditions, 2 February 1911. Photographs of skull have been examined.

Type Locality: Lönnberg (1913, p. 9) says 'caught in crack of the earth on a plain near Noonkambah . . .'.

Planigale ingrami brunneus Troughton, 1928

Holotype: AM M2174, skull and carcase in alcohol, adult female, donated by Mr F. L. Berney. The holotype has been examined.

Type Locality: Troughton (1928, p. 285) gives 'Wyangarie, on the Flinders River, Richmond district, northern Queensland.'

Material Examined

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Richmond (e.g. J7655); Leslew Downs, nr Richmond (JM824); Alex Ck, approx. 8 km from Leslew Downs (JM763); Wyangerie, nr Richmond (AM M2174); Major Ck, nr Townsville (JM764); Red Falls, nr Lolworth Ck, 88 km NW. Charters Towers (Qd Museum); Charters Towers (Department Primary Industries, Townsville); Karumba, nr Normanton (e.g. AM M8468); Old Normanton (e.g. C3260).

Northern Territory: 200 km W. Burketown (e.g. AM M5022); owl pellets, Brunette Downs (N.T. Museum and noted in Parker 1973).

Western Australia: Ord River area (WAM M2846); Argyle Downs Stn (W.A. Museum); Wotjalum Mission, nr Derby (WAM M3191); cave surface, approx. 16 km SE. Fitzroy Crossing (e.g. 71.12.30); cave, Windjana Gorge (72.9.64); cave, between Kununarra and Ninbing Stn (JM827).

Distribution of specimens shown in Fig. 3.

Diagnosis

Smallest species, also differing from other species in having tail commonly longer than head and body and in certain external, cranial, and dental ratios including highest mean BL/M^{1-3} and NW/NL. Also differs from *P. maculata* and *P. novaeguineae* in lower mean SD/IO, PN/NL and higher mean FM/SD. Also differs from *P. tenuirostris* in lower mean SD/IO. Also differs from *P. gilesi* in having P4, and lower mean PN/NL.

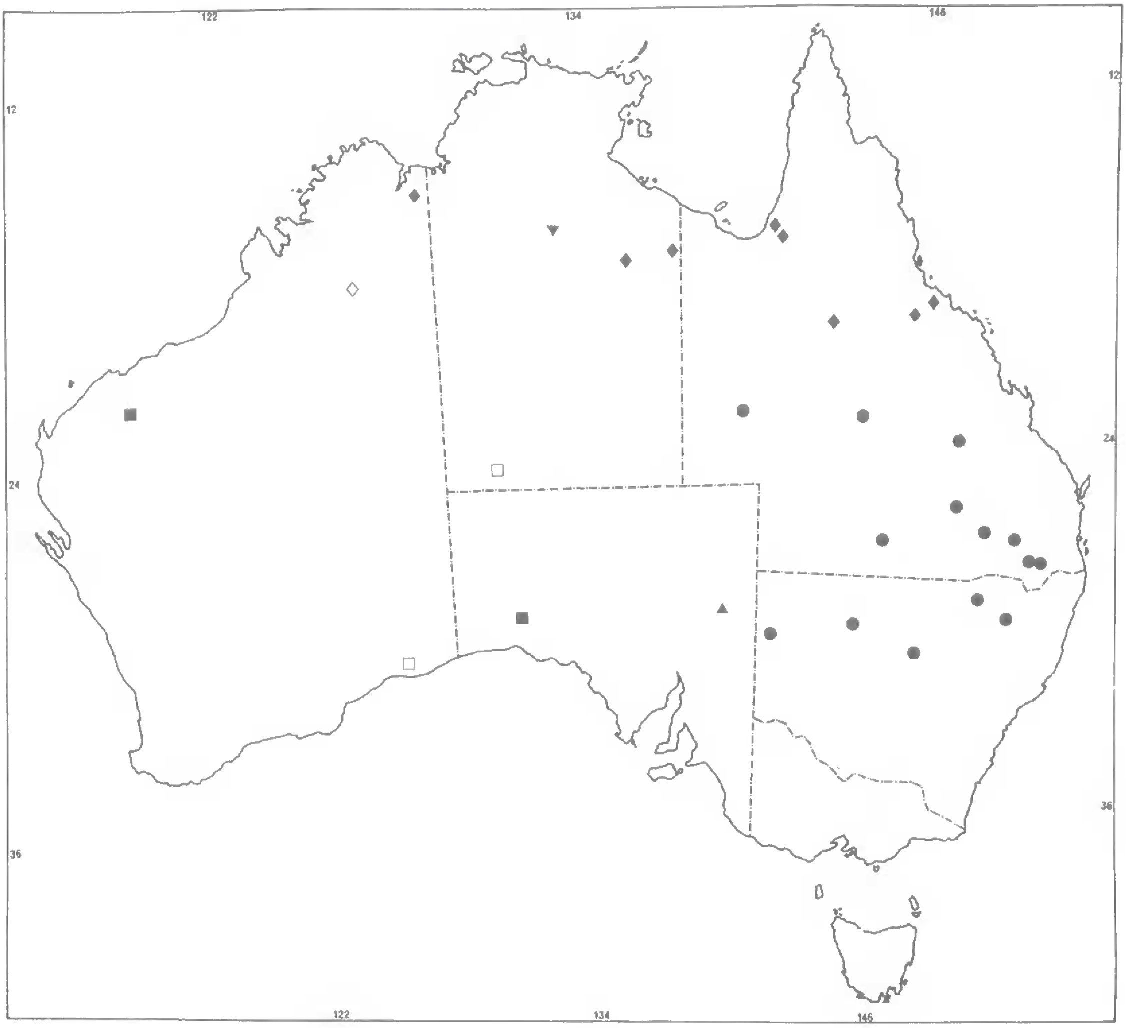

FIG. 3: Distribution of *Planigale ingrami* (solid diamonds represent modern specimens examined; hollow diamonds represent cave specimens examined; inverted solid triangle represents record given by Van Deusen 1969), *P. tenuirostris* (solid dots represent modern specimens examined; solid triangle represents record given by Aitken 1971), and *Planigale* sp. (solid squares represent specimens examined from Ooldea and Tambrey; hollow squares represent cave specimens from Ayers Rock and Madura).

DESCRIPTION

Tail invariably thin. Tail-vent length generally longer than head-body length, and longer in *subtilissima* than *brunneus* and typical forms. Thomas's (1906b) description of body measurements of lectotype and paratype of typical form, give mean TV/HB value of 0·75. Not clear from Thomas's description if all specimens (Thomas indicates five) collected by Stalker had shorter tails than head-body measurements. He states (p. 541) 'Tail of medium length . . .'.

Supratragus of ear relatively long, compared with other species and relatively longer in *subtilissima* than typical form.

Six to 10 nipples have been recorded. Heinsohn (1970) notes some individuals with 12 young. Three individuals of *subtilissima* form have 10 nipples, fourth appears to have only 9 and is presumably abnormal. Holotype *P. i. brunneus* has 6 nipples.

Pouch morphology may distinguish *subtilissima* from other forms (as suggested by Woolley 1974), although *subtilissima* form not unique in possession of accessory anterior pockets. Less well-developed pockets occur in *P. ingrami* from Richmond, and may occur in all forms but possibility cannot at present be checked. More detailed examination is required of possible changes in pouch morphology as a function of reproductive condition.

Thomas (1906b, p. 541) says of typical form 'General colour above not unlike that of paler wild-living forms of *Mus musculus*, something between Ridgway's "wood-brown" and "broccoli-brown", the hairs slaty grey, with pale tips . . . Under surface paler, with a yellowish tinge . . . the hairs slaty at base except on the chin. Crown like back. Cheeks and chin whitish. A whitish-buffy line just over each eye.' Two females of *subtilissima* form examined live are not identically coloured: one much darker than other with black nose; other noticeably lighter with caramel-coloured nose. This variation not clearly attributable to different habitats and may represent normal intra-specific variation. Heinsohn (1970) says of *P. ingrami* from near Townsville that individuals from areas of black basalt rock tend to be black, whereas those from non-basalt areas are grey or grey-brown. Individuals of *brunnea* form may be distinguished from typical form by brown basal fur.

Absolute size of many dental and cranial characters comparable with *P. tenuirostris*, smaller than *P. maculata*, *P. gilesi* and *P. novaeguineae*. Mean M_{1-3} length *P. ingrami* 3·1 compared with 3·0 for *P. tenuirostris*, 3·6 for *P. gilesi*, 3·6 for *P. maculata*, and 4·1 for *P. novaeguineae*. Various mean cranial ratio values distinctive as follows: mean SD/IO value comparable with that of *P. gilesi*, lower than that of *P. tenuirostris* and much lower than that of *P. maculata* and *P. novaeguineae*, indicating very flat head and broad interorbital region of *P. ingrami*; mean BL/M^{1-3} value *P. ingrami* higher than all other species, reflecting proportionately long periotic and alisphenoid bullae; mean FM/SD value comparable with *P. gilesi* and *P. tenuirostris* but considerably larger than *P. maculata* and *P. novaeguineae*; mean NW/NL value higher than that of any other species, indicating very short and wide (posteriorly) nasals of *P. ingrami*; mean PN/NL value comparable with that of *P. tenuirostris* but smaller than that of *P. gilesi*, *P. maculata*, and *P. novaeguineae*. Intraspecifically, *subtilissima* form generally distinguishable from typical form by relatively smaller P^4. Difference in crown height between P^4 and P^1 noticeable, but less than two times height of P^1. One individual (AM M5021) of typical form from 200 km W. Burketown similar, with only slightly enlarged P^4. Both forms have well-developed posterior P^4 talon.

Specimens of *brunnea* form have highest mean FM/SD value of any *Planigale* population, reflecting relatively very flat heads and wide foramen magnum. This form also distinguished from *subtilissima* form by higher mean PMX–NAS/NL value and relatively longer lower premolar row. P^4 also relatively larger.

Discussion

Cranial measurements given by Thomas (1906b) for *P. ingrami* are similar to those of specimens referred in the present study to *P. ingrami*. The very flat head and wide interorbital width values are very similar to those of specimens from Richmond and 200 km W. of Burketown. The SD/IO value of the lectotype, 0·87, is the same as that of the mean value for specimens from 200 km W. of Burketown and comparable with that of specimens of the *brunnea* form from Richmond. It is also comparable with the mean value for individuals of the *subtilissima* form. This feature, in conjunction with many other similar cranial and dental ratios and absolute measurements, indicates the general similarity of the type specimen to those of other samples regarded in this study as *p. ingrami*.

Heinsohn (1970) records several individuals of *P. ingrami* from the Townsville area. Examination of these specimens (including JM823 and JM764) indicates that *P. maculata* and *P. ingrami* are sympatric at Major Creek, Woodstock. Marlow (1962) records *P. ingrami* (AM M8148) from Coen, Queensland. This specimen has been examined and appears to be a juvenile *P. maculata*. Specimens referred by Fleay (1965, 1967) to *P. ingrami* probably represent *P. maculata* and possibly include some *P. tenuirostris*. Ride (1970) refers specimens from Laverton, Western Australia to *Planigale* cf. *P. ingrami* (plate 35). These specimens have been described as *Ningaui ridei* (Archer 1975). Ride (1970, p. 120) also refers to *P. ingrami* from '. . . Kimberley and central W.A. . . .'. This material has been examined and, like all modern specimens of *Planigale ingrami* examined from the Kimberley region, appears to represent the *subtilissima* form of *P. ingrami*. One fossil sample from the southeastern edge of the Kimberley region is unusual (see below).

Forms of *P. ingrami:* There are at least two allopatric forms of *P. ingrami*. The typical form includes samples from the Barkly Tableland, in an area 200 km west of Burketown; and other areas in northeastern Queensland as far east as the Townsville area. The *subtilissima* form includes samples from the Kimberley Region. The *brunnea* form includes samples from the Richmond area. Specimens from Old Normanton and Karumba, Queensland, are not clearly referable to any of these three and either represent a fourth form of *P. ingrami* or perhaps a mixed sample of more than one species. No attempt has been made here to assess the possible statistical basis for recognizing subspecies. Use of the formal names for these allopatric forms here is a matter of convenience and must not be interpreted as recognition of their subspecific status.

Lönnberg (1913) describes *Phascogale subtilissima* on the basis of a specimen that was shown by Tate (1947) to be juvenile. Tate considers the *subtilissima* form to be a race of *ingrami* and in this view is followed by Marlow (1968). Troughton (1928, 1967) and Ride (1970) regard it as a full species. Close similarity has been noted here between specimens of the *subtilissima* and typical forms. Although modern and fossil Kimberley specimens demonstrate morphological extremes, they are in most respects just one step beyond specimens from 200 km west of Burketown, which are also geographically closest to the Kimberley population. A cline may exist which links animals from the area west of Burketown, via the Barkly Tableland, to the Kimberley region. More specimens are required to test this possibility.

Fossil specimens (including 72.9.65 and 71.12.29–31) collected from surficial cave deposits in the southern Kimberley region, associated with a small mammal fauna which will be described elsewhere, represent at least nine individuals. They differ in some absolute measurements from specimens of the *subtilissima* form including mean I_1–M_4 length of the fossil specimens which is 5·9 mm as opposed to 6·7 mm for the *subtilissima* form. This results in a $(I_1\text{–}M_4)\text{–}(M_{1-4})/(M_{1-3})$ value of 0·83 for the fossil sample as opposed to 0·90 for the modern sample. This is also the lowest figure for any *Planigale* population. Further, mean length of the dentary of the fossil sample, 10·6 mm, is less than that of all other *Planigale*.

Troughton (1928) considers the *brunnea* form to differ from the typical form in possessing brown basal fur, longer tail, premaxillary vacuity which extends posteriorly to the middle of the C^1 alveolus, clear maxillary vacuity, P^1 barely two thirds of the height of P^3 rather than subequal, and broader nasals. Topotypical specimens J7655–6, give an idea of variation unavailable to Troughton. Both Queensland Museum specimens have premaxillary vacuities which extend beyond the level of the anterior edge of the C^1. This is an almost universal condition in *P. ingrami* examined in the present study. It seems likely that the type of the species is unusual in this respect (Thomas 1906b). Both Richmond specimens and all *Planigale* specimens examined have small, distinct maxillary fenestra, and this is not a useful diagnostic character for any subgeneric taxonomic rank. If these vacuities are not apparent, palatal skin has not been removed from the bony palate. Regarding premolar gradient, in J2655 P^3 is only slightly larger than P^1 and in J7656 P^3 is almost equal to P^1 in height. Regarding relative nasal breadth, the NW/NL value of the holotype of *brunneus*, using Troughton's (1928) measurements, is 0·49. This value for J7655 is also 0·49, while the measure for J7656 is 0·43. Regarding tail length, although measurements of J7655–6 are unknown, other samples serve to show that there is considerable variation in this character (see Table 2). This leaves basal fur colour as a possibly useful diagnostic character. This condition is indeterminable in J7655–6. However, Thomas (1906b) notes variation in fur colour. It therefore seems unlikely that the *brunnea* form is differentiable from the typical form using characters given by Troughton (1928), with the possible exception of basal fur colour.

Specimens from Old Normanton (C3259–60) and Karumba (AM M8467–9, M9144) are so variable that they may represent more than one species. Two specimens (both males) AM M8468 and AM M8469 from Karumba are more robust and broader-skulled than the third, AM M8467 (also male), from this locality. Specimens from Old Normanton (one male, one female) resemble in most respects AM M8467.

Habitat and Reproduction

Typical *ingrami:* In N.T. they inhabit area around Alexandria draining inwards to Polygonum swamp (Thomas 1906b); at locality 200 km W. Burketown, they occur in tussocky grass, dry swamps and along perennial streams flowing out of the coastal ranges westward from Burketown (Troughton 1967); at New Castle Waters, one was found under bark near a small stream (Van Deusen 1969); generally not uncommon on blacksoil plains, dry swamps and perennial watercourses of the Gulf drainage (Parker 1973). In Qd, 137 km SW. Townsville, one was found drinking from a rock pool (Heinsohn 1970).

In N.T., 200 km W. Burketown, they are said (Albert De Lestang, letter in Queensland Museum dated 8 October 1930) to breed in February to April, producing litters of 4 to 6 young. In NE.Qd they have litters of 4 to 12, reproduction occurring around December to March (Heinsohn 1970).

In captivity, an individual of the typical form constructed a series of covered runways and a hollow nest chamber in dry grass (Heinsohn 1970).

Subtilissima form: In W.A. they inhabit tussocks of grass near the Kimberley Research Stn and were also collected from piles of wet decomposing grass (Rudeforth 1950 and pers. comm.); on isolated hills on Argyle Downs Stn, while the waters of Lake Argyle were rising, they were collected from clumps of spinifex (Dr D. Kitchener and Mr W. H. Butler, pers. comm.).

One or two females from Argyle Downs Stn collected live in December–January 1971–2 had an unspecified number of young about 0·5 cm long in her pouch. A single juvenile was preserved before the mother was transported to Perth. She evidently consumed the remaining young in transit. During January, the other female's pouch underwent enlargement, elongation of pouch hairs and, towards the end of February, regression. No juveniles were born. Woolley (1974) notes changes in pouch morphology of these same individuals and concludes that this form breeds in summer months, unlike the majority of dasyurids.

Brunnea form: Habitat unknown. Holotype has pouch young but month of collection is not recorded.

Old Normanton: Habitat unknown. One specimen (AM M9144) with 8 (or possibly 9) nipples died June 1965. The pouch was developing but clearly not in breeding condition.

Planigale tenuirostris Troughton
(Plate 48)

Planigale tenuirostris Troughton, 1928, pp. 285–7.

Type

Holotype: AM M3933, skull and carcase in alcohol, adult female, collected by R. Helms in May or June 1890. The holotype has been examined.

Type Locality: Troughton (1928, p. 287) says 'Collected at Bourke or Wilcannia, New South Wales, during the Darling River floods.'

Material Examined

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Cunnamulla (AM M6957); Warwick (J7559); Pittsworth (J3096); Roma (J3824); 16 km NE. Longreach (J17549); Glenmorgan (J10109); Belmont, via Rockhampton (J14089).

New South Wales: Bourke or Wilcannia, Darling River (AM M3933); Bellata (AM M6879); Cullubri, 43 km SSE. Nyngan (AM M8151); Fowlers Gap (e.g. JM831).

Distribution of specimens shown in Fig. 3.

Diagnosis

Small, very similar to *P. ingrami* but differs in relatively shorter supratragus of ear; tail being generally shorter than head-body length; and in several cranial ratios including lower mean BL/M^{1-3} and NW/NL, BW/M^{1-3}, BL/M^{1-3} and higher mean SD/IO, SD/ZW, and BL/ZW. Differs from *P. novaeguineae* and *P. maculata* in being smaller; in having relatively reduced transverse canal foramina; smaller stylar cusp D on M^3; longer head; wider interorbital distance; and in several cranial ratios including lower mean BL/ZW, PN/NL, SD/IO and higher mean NW/ZW, BL/ZW, BL/M^{1-3}, FM/SD, and FM/ZW. Differs from *P. gilesi* in having P4.

Description

Mean TV/HV value, 0·87, indicates relatively short-tailed condition.

Mean ST/E value, 0·28, lowest of any *Planigale* except *P. maculata* from Aurukun Mission. Mean absolute supratragus length, 2·6 mm, shortest.

Troughton (1928) notes holotype has 11 nipples but suggests normal number is 10. J7559 from Warwick, Queensland, has 7. J3096 from Pittsworth, Queensland, has 8.

Mean BL/ZW value highest indicating relative dolichocephaly. Mean NW/NL value lower than any *P. ingrami*, demonstrating relatively narrow nasals. Other differences indicated in Tables 1–2.

Discussion

Troughton (1928) describes characters which he believes are useful in diagnosing *P. tenuirostris*. Having examined larger series of specimens of *P. ingrami* than were available to Troughton, it is clear that some of these characters are also variably present in *P. ingrami*. For example, Troughton (1928) says *P. tenuirostris* has 10 or 12 nipples in contrast to *P. ingrami* which has 6. As noted above, the *subtilissima* form may have 10 nipples, the typical form of *P. ingrami* from 200 km west of Burketown may have 10, the typical form of *P. ingrami* from near Townsville (Heinsohn 1970) may have 6 to 12, *P. gilesi* has 12 (Aitken 1972), and some *P. maculata* may have 8 to 15 (Fleay 1965, 1967, Davies 1960). Troughton (1928) considers that *P. tenuirostris* has more elongate premaxillae than *P. ingrami*. In some cases, this appears to be true. However, mean premaxilla-nasal contact length, a measure of this character, is 2·4 mm in specimens of *P. tenuirostris*, and 2·3 mm in specimens of *P. ingrami* from near Richmond, indicating little, if any, difference. Troughton (1928) describes P^1 as being two-thirds the size of

P^3 in *P. tenuirostris* and subequal in typical *P. ingrami* (Thomas 1906). This character appears variable in *P. ingrami* (see above) and *P. tenuirostris*. Troughton (1928) considers *P. tenuirostris* to differ from the *brunnea* form of *P. ingrami* in its narrower hind foot, a condition which may relate to some circumstance of death. Among specimens of *P. ingrami*, AM M5022 has a hind foot noticeably wider distally than AM M4744 from the same locality. The widely spread foot of AM M5022 suggests the animal may have died and been fixed in muscular spasm. Finally, Troughton (1928) considers *P. tenuirostris* to differ from the *brunnea* form of *P. ingrami* in possessing a posterior notch on the lower part of the pinna of the ear. On the basis of larger series, this appears variable in both *P. tenuirostris* (e.g. slight or absent in AM M7313 and pronounced in holotype) and *P. ingrami* (small notch present in AM M5022 but not present in holotype of *P.i. brunneus*).

Van Deusen (in Fleay 1965) suggests *P. tenuirostris* may be a race of *P. ingrami*. The evidence seems inadequate to decide one way or the other. The present study only suggests that specimens referred here to *P. tenuirostris* exhibit some extremes in size and proportion, and most appear to inhabit more central or arid areas.

Marlow (1958) refers some specimens (AM M7033, M7393, M7819 and M7820) to this species from New South Wales. Aitken (1971) refers these to *P. gilesi*.

Habitat and Reproduction

Aitken (1972) notes *P. tenuirostris* (AM M6879 and AM M7313) is sympatric with *P. gilesi* (AM M7033) from Bellata, New South Wales, and that (1971) a dehydrated specimen of *P. tenuirostris* (SAM M8405) was found at the bottom of a disused stone tank at Mulga Creek Well, near the northeastern tip of the Flinders Range, South Australia. In the same tank was a specimen of *Sminthopsis crassicaudata*.

Troughton (1928) notes the holotype, collected during the Darling River floods in May or June, 1890, has a well-developed pouch with enlarged nipples.

Holotype

The holotype has been examined. Troughton (1928, fig. 2) illustrates the ear, nose, hind foot, and skull of the holotype. Specimen numbers given by Troughton appear to be confused. The holotype is stated to be AM M3856, but AM M3933 in the Australian Museum is labelled as the holotype. AM M3856 is (pers. comm. Mr B. Marlow, 1975) listed in the Australian Museum catalogue as *Pteropus poliocephalus* from Tamborine, south Queensland.

The **Planigale gilesi** group

This group contains only *P. gilesi* Aitken.

Planigale gilesi Aitken
(Plate 49)

Planigale gilesi Aitken, 1972, pp. 1–14.

Type

Holotype: SAM M8046, dry skin and skull, torso in spirit, adult male, collected by messrs P. Aitken, A. Kowanko, J. Forrest and J. Howard, 29 June 1969. The holotype has been examined.

Type Locality: Aitken (1972, p. 1) gives 'No. 3 Bore, Pastoral Property of Anna Creek, South Australia (lat. 28° 18′S, long. 136° 29′ 40″E).'

Material Examined

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Durrie Stn, 97 km E. Birdsville (J21973).

South Australia: Anna Creek (e.g. SAM M8406).

New South Wales: Bellata (e.g. AM M7033); Brewarrina (e.g. AM M7819); Fowlers Gap; Mt King, 27 km N. Tibooburra (AM M9829).

Distribution of specimens shown in Fig. 2.

Diagnosis

Large species of *Planigale* differing from all others by having only two upper and lower premolars on each side as adult condition.

Description

Tail thin to slightly incrassated. Shorter than head and body length. Mean TV/HB value 0·96.

Supratragus of ear relatively long. Mean ST/E value 0·36.

Apical granules of interdigital pads of hindfoot have striae which do not reflect incident light and hence do not occur as ridges on surface of granule.

Aitken (1972) records twelve nipples.

Cranium wide and very flat. Parietal horns extend anteriorly to level near anterior end of cerebral hemispheres. Mean SD/IO value, SD/C^1–M^4 and several other cranial and dental ratios (see Table 2) very similar to those of otherwise smaller *P. ingrami*.

Discussion

P. gilesi is the most distinctive species of the genus because of the reduced premolar number. When premolar reduction or loss occurs in other dasyurids (e.g. some *Antechinus*, *Neophascogale* Stein, 1933, *Phascolosorex* Matschie, 1916, *Myoictis* Gray, 1858, *Dasycercus*, *Dasyuroides*, *Dasyurus* Matschie, 1916) invariably the posterior premolar is reduced. This predisposition to reduce or lose P4 in dasyurids has previously been noted (e.g. Thomas 1887, Bensley 1903, Tate 1947). In genera in which only some species have lost premolars, others show reduction of P4. For example, all *Antechinus rosamondae* Ride, 1964 have two premolars above and below. Some individuals of *A. macdonnellensis* (Spencer, 1896) show the same condition. Others show a small P4 above and below. Still others lack P4 altogether. There is therefore a structural gradient of loss within the genus. In *Planigale*, two trends in premolar size are evident. In all species P_1 and P^1 are reduced, possibly the result of the very large canines, and (except in *P. gilesi*) P_4 is markedly reduced while P^4 is grossly enlarged into a tall shearing blade. Only the *subtilissima* form of *P. ingrami* does not show gross enlargement of P^4, but even here, P^4 is larger than P^3. If these trends in *Planigale* are used to interpret tooth loss in *P. gilesi*, the most logical conclusion is that P^1 and P_4 have been lost. If this were so, the anterior upper premolar (P^3) should shear behind the posterior lower premolar (P_3), a situation which does not exist. If P^1 and P_4 were lost, there must have been an intermediate stage in which premolars did not occlude in order that the anterior upper premolar and posterior lower premolar could bypass one another. Such an intermediate stage of non-occlusion is improbable and it is concluded that *P. gilesi*, like all other dasyurids which exhibit premolar reduction, has lost P^4 and P_4.

Loss of P^4 and P_4 in *P. gilesi*, in spite of the trend for reduction of P^1 rather than P^4 in other *Planigale*, indicates the magnitude of the structural gap between *P. gilesi* and other *Planigale*.

Habitat and Reproduction

Aitken (1972) describes the habitat as bullrush and sedge plant associations developed around a bore drain in an area where average annual rainfall is less than 125 mm per year. Other sympatric species include *Canis familiaris*, *Sminthopsis froggatti*, *Pseudomys desertor*, *Rattus villosissimus*, *Mus musculus*, and introduced mammals such as rabbits, foxes, cats, camels, horses and cows. Aitken (1972) concludes *P. gilesi* is at least partially insectivorous.

None of the specimens examined by Aitken (1972) indicate the breeding season. Of two females with undeveloped pouches, AM M7033 (according to the label) was collected in June (Aitken says 27 Feb.) and SAM M8411 was collected in August.

Holotype: The holotype has been examined. The skull and dentary are figured by Aitken (1972, plate 3).

Planigale, incertae sedis

Two specimens of *Planigale* examined in this study are not clearly referable to any described species. Both are damaged, and until better material comes to hand, they should not be named. A third form is described by Lundelius and Turnbull (1973).

J16732

A juvenile collected by A. S. Le Souef from Ooldea, Transcontinental Railway, South Australia (Fig. 3). Because it is juvenile (P_4 has not completely erupted), most cranial and dental measures cannot be meaningfully compared with those of adults of other species. It is most similar to *P. tenuirostris*. The bullae appear to be very much smaller than those of *P. tenuirostris*. P_4 (excavated) is 0·45 mm long; P_3 is 0·70 mm long; P_1 is 0·60 mm long.

WAM M3432 (Plate 50)

This specimen, the basis of Ride's (1970, p. 120) recognition of *Planigale maculata* in Western Australia, consists of a broken skull and somewhat damaged skin of an old adult male, collected by Mr W. H. Butler on 3 August 1958, from Tambrey, Coolawanyah Station, Hammersley District of Western Australia (Fig. 3). P_4 is double-rooted, a very unusual condition in *Planigale*. M^{1-3}/ZW value, 0·32, is lower than the mean of any other *Planigale* population. $(C^1 - M^4) - (M^{1-4})/M^{1-3}$ value, 0·82, is larger than the mean for any other *Planigale* population. This specimen may represent an unnamed species of *Planigale* but the specimen is too incomplete and isolated to permit adequate comparisons. P_4 is 0·56 mm long; P_3 0·65 mm long; and P_1 0·60 mm long.

The Madura Form

Lundelius and Turnbull (1973) describe a Quaternary *Planigale* from Madura Cave, on the Roe Plain of the Western Australian Nullarbor (Fig. 3). After comparing it with several specimens of *P. ingrami* and one specimen of *P. maculata*, they conclude (p. 27) '. . . the Madura Cave material cannot be referred to any of the described species of pygmy antechinuses', and consider (p. 18) it is similar to *P. maculata* in having P^1 crowded out of alignment in the tooth row, a feature which contrasts with *P. ingrami*. An examination of larger series of specimens than those available to Lundelius and Turnbull suggest this character is variable in *P. ingrami* and *P. maculata*. Two out of 5 modern *P. ingrami* have P^1 crowded out of alignment (e.g. J7656) and 1 (J17549) has LP^1 crowded out of line while RP^1 is straight. In 2 other specimens, P^1 is straight on both sides. In 10 *P. maculata* (a single sample from Mt Molloy), 3 specimens (e.g. J16730) have P^1 crown straight, 5 (e.g. J16481) have the crown slightly crowded out of alignment, and 2 (e.g. J16729) have the crown markedly crowded out of alignment. In *P. tenuirostris* all 4 specimens examined have the P^1 crown straight, as does the single specimen of *P. gilesi* checked for this character. Lundelius and Turnbull also suggest (p. 20) that the Madura *Planigale* resembles *P. maculata* in having a less-indented ectoloph immediately anterior to stylar cusp D (their mesostyle) than is present in *P. ingrami*. An examination of this character in 10 *P. ingrami* and 10 *P. maculata* similarly suggests the character is not constant in either of the two modern species. In J15891, the ectoloph is as deeply indented as in most *P. ingrami* and more deeply indented than others. It reveals that stylar cusp D is in general larger in *P. maculata* than *P. ingrami* and in this respect the Madura *Planigale* more closely resembles the latter. Lundelius and Turnbull also note (p. 22) that in the Madura *Planigale*, P_4 is generally straight while P_1 is crowded out of alignment, and in this respect it is unlike *P. ingrami*. In a series of modern *P. ingrami* examined in this study, orientation of P_4 appears to be variable. In J17549, P_4 is straight while P_3 and P_1 are slightly crowded out of alignment. In J7656 and J7655, P_4 is crowded out of alignment. In *P. maculata*, some specimens have P_4 straight (e.g. J16477, J16730), slightly turned (e.g. J16729, J16481), or markedly turned (e.g. J16482, J15891). Similar variation occurs in *P. tenuirostris*. The Madura *Planigale* is very distinctive in regard to the large size of P_4, as noted by Lundelius and Turnbull. No P_4 of any modern *Planigale* examined in the present study is of comparable length, not even the two-rooted P_4 of WAM M3432.

Summary of Resemblance Within *Planigale*

Typical *P. maculata* and *P. novaeguineae* are very similar, and may prove conspecific. A general trend of increasing size exists in coastal populations north from New South Wales into New Guinea. Other trends such as reduction in size of alisphenoid bullae are also demonstrated. *P. novaeguineae* appears, in most respects, to represent no more than one end of this cline. Northern Territory and northwestern Queensland *P. maculata* (possibly all referable to *P. m. sinualis*) are distinct from the typical form.

P. ingrami and *P. tenuirostris* are similar and it is not clear that they are separate species. These two forms are similar to *P. gilesi*, which because of premolar loss involving a reversal of a trend developed in the remaining species of the genus, is otherwise very distinct from all other *Planigale*.

The *subtilissima* form of *P. ingrami* is distinctive, while the *brunnea* form may be identical with the typical form of *P. ingrami*.

There may be additional undescribed forms of *Planigale* represented by single specimens or small samples, at present too inadequate to assess taxonomically.

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APPENDIX

Since this paper went to press I have had an opportunity to examine specimens of *Planigale* in the United States and England, and can make the following comments.

Specimens in the collections of the American Museum of Natural History include:

P. maculata (AMNH 160075-6, near Townsville, Qd. AMNH 193959, Gunalda, N. of Gympie, Qd. AMNH 160374, Monto, Qd. AMNH 18380, the *sinualis* form, Red Bank Mine, 18 miles (29 km) W. Wollogarang, N.T.). AMNH 193959 and 160374 were donated by Mr D. Fleay and support the suggestion made above that at least some of the specimens reported by Fleay (1965) represent *P. maculata* rather than *P. ingrami*.

P. novaeguineae (AMNH 108561, Holotype, Rona Falls, nr Port Moresby, Papua: measurements: C^1–M^4, 8·2; M^{1-4}, 4·9; M^{1-3}, 4·3; I_1–M_4, 9·5; M_{1-4}, 5·3; M_{1-3}, 4·0; nasal length, 9·2; maximum width of nasals, 4·0; minimum width of nasals, 1·7; pmx-nasal suture, 4·1; the skull is badly smashed and lacks RI_{1-3}, RP_1, RP_4, LI_1–P_4, and RM^{2-4}; foot pads are faintly striated, clearly the result of dehydration).

P. ingrami (AMNH 160313, Karumba, Qd, appears to represent this species but I have not examined the skull so reference here is tentative).

Specimens in the collections of the British Museum (Natural History) include:

P. maculata (BM53.10.22.21, Holotype, Clarence R., Moreton Bay, Qd: measurements: C^1–M^4, 6·7; M^{1-4}, 4·0; M^{1-3}, 3·7; R-LM^3, 6·2; IPVD, 4·5; I_1-M_4, 7·3; M_{1-4}, 4·6; M_{1-3}, 3·4; nasal length, 6·8; minimum width of nasals, 0·8; pmx-nasal suture, 2·9; the skull is only represented by a rostrum with damaged lower jaws, and lacks RP^1 and LP_1. Skin with number 53.10.22.21. is type and has locality as Clarence R., Moreton Bay; vague white spots are apparent on ventral side and flanks; it has damaged feet and scrotal area. BM54.10.21.5, Holotype of *minutissima*, Cressbrook, N.S.W.: measurements: ZW, 10·5; C^1–M^4, 6·8; M^{1-4}, 4·2; M^{1-3}, 3·8; R–LM^3, 6·4; IO, 4·1; IPVD, 4·4; DL, 13·5; I_1–M_4, 7·7; M_{1-4}, 4·4; M_{1-3}, 3·4; C–AP, 4·0; C–AR, 4·4; SD, 5·3; nasal length, 7·1; maximum nasal width, 3·2; minimum nasal width, 1·2; pmx-nasal suture, 2·5; the rear of skull is badly damaged. Skin with number 53.10.22.20, is type and has locality as Cressbrook, Moreton Bay; it has damaged feet and ventral surface; BM26.3.11.194, Holotype of *sinualis*, Groote Eylandt: measurements of this juvenile with M^3 erupting were not made except for M_{1-3} which is 3·7; skin is in good condition. BM76.3.29.2, Peak Downs, Qd. BM91.6.28.1, N.S.W. BM25.8.1.133, locality?. BM75.14.1.23.5–6, Gin Gin, Qd).

P. novaeguineae (BM 73.145, Mt Eriama, about 10 miles (16 km) from Port Moresby and 8 miles (13 km) from Rouna, Papua).

P. ingrami (BM6.3.9.77, Holotype, Buchanan, Alexandria, N.T.: measurements: BL, 17·0; ZW, 9·4; OBW, 7·2; IBW, 2·3; C^1–M^4, 6·0; M^{1-4}, 3·5; M^{1-3}, 3·1; R–LM^3, 5·7; IO, 3·9; IPVD, 3·9; DL, 12·9; I_1–M_4, 6·8; M_{1-4}, 3·9; M_{1-3}, 3·0; C–AP, 3·7; C–AR, 3·7; SD, 3·6; bullar length, 4·9; nasal length, 6·7; maximum nasal width, 2·8; minimum nasal width, 1·0; pmx-nasal suture, 2·5; FM, 3·7; skull represents very old individual with worn teeth and lacks RM^2 although loss occurred during life; skin is in good condition. BM6.3.9.76, BM6.3.9.78, Buchanan, Alexandria, N.T.. BM6.3.9.79, Bluff Hole, Alexandria, N.T.. BM6.3.9.80, Alexandria, N.T.. BM25.4.9.8, the *subtilissima* form, Derby, W.A.).

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Abbreviations: BL, basicranial length; ZW, zygomatic width; OBW, outside bullar width; IBW, inside bullar width; FM, maximum width foramen magnum; IO, minimum interorbital width; VV, inter-palatal vacuity distance; DL, dentary length; C–AP, articular condyle to anterior border of ascending ramus; C–AR, articular condyle to tip of angular process; NL, nasal length; NW, maximum nasal width; NWMN, minimum nasal width; PN, nasal-premaxillary suture length; PLF–AB, bullar length from posterior lacerate foramen to anterior end alisphenoid tympanic wing; SD, skull depth; N, number of specimens in sample; $x \pm \tau$, sample mean $\pm$ one standard error; O.R., observed range; s, standard deviation; CV, coefficient of variation.

TABLE 1: Absolute Measurements in Species of *Planigale*

	N	x̄ ± σ	OR	s	CV	N	x̄ ± σ	OR	s	CV
	Planigale novaguineae					P. maculata (total)				
BL	2	21.4±.98	20.0-22.7	1.38	6.46	38	18.3±.14	16.4-20.2	0.86	4.67
ZW	2	12.3±.75	11.5-13.1	1.06	8.64	40	10.6±.10	9.3-12.0	0.66	6.24
OBW	2	8.1±.57	7.6- 8.5	0.80	9.88	40	7.3±.07	6.7- 8.3	0.41	5.68
IBW	2	3.2±.46	2.9- 3.5	0.65	20.35	38	2.6±.04	2.1- 3.1	0.25	9.60
C^1-M^4	2	8.3±.50	7.9- 8.6	0.70	8.52	43	6.9±.05	6.4- 7.6	0.31	4.49
M^{1-4}	2	4.8±.33	4.6- 4.9	0.47	9.84	44	4.3±.02	4.0- 4.6	0.15	3.47
M^{1-3}	2	4.3±.27	4.2- 4.4	0.38	8.73	48	3.9±.02	3.7- 4.2	0.13	3.29
R-LM^3	2	7.2±.46	6.9- 7.5	0.65	9.04	41	6.4±.04	5.8- 7.1	0.29	4.46
FM	2	4.3±.38	4.1- 4.5	0.53	12.35	37	4.0±.04	3.5- 4.2	0.25	6.02
IO	2	4.9±.33	4.7- 5.0	0.47	9.64	42	4.2±.04	3.8- 4.8	0.24	5.72
VV	2	5.6±.75	4.8- 6.4	1.06	18.98	42	4.5±.06	3.6- 5.3	0.38	8.46
DL	2	16.6±.78	15.7-17.4	1.10	6.61	45	14.0±.13	12.6-15.7	0.84	5.99
I_1-M_4	2	9.6±.53	9.2-10.0	0.75	7.83	44	8.1±.06	7.5- 8.9	0.37	4.54
M_{1-4}	2	5.4±.33	5.2- 5.5	0.47	8.74	44	4.7±.02	4.4- 5.0	0.16	3.33
M_{1-3}	2	4.1±.33	3.9- 4.2	0.47	11.52	46	3.6±.02	3.3- 3.9	0.16	4.57
C-AP	2	4.7±.33	4.5- 4.8	0.47	10.05	42	4.1±.04	3.7- 4.6	0.23	5.62
C-AR	2	5.0±.53	4.6- 5.4	0.75	15.03	42	4.2±.04	3.5- 4.7	0.29	6.83
NL	2	9.0±.65	8.4- 9.6	0.92	10.32	40	7.4±.09	6.4- 8.4	0.54	7.29
NW	2	3.8±.27	3.7- 3.9	0.38	9.88	41	2.9±.04	2.3- 3.5	0.28	9.49
NWMN	2	1.6±.22	1.5- 1.6	0.32	19.76	40	1.3±.02	1.1- 1.6	0.13	10.38
PN	2	3.5±.35	2.9- 4.0	0.50	14.17	39	3.0±.06	2.3- 3.6	0.37	12.30
PLF-AB	2	4.7±.22	4.6- 4.7	0.32	6.73	37	4.4±.04	3.8- 4.8	0.22	4.99
SD	2	6.0±.50	5.6- 6.3	0.71	11.79	41	4.8±.04	4.2- 5.4	0.29	5.96
	P. m.(Qld)					P. m.(Mt Molloy)				
BL	23	18.3± .19	16.9-20.2	0.91	4.99	7	18.9±.35	18.0-20.0	0.94	4.97
ZW	24	10.6±1.34	9.3-12.0	0.70	6.57	7	11.1±.22	10.2-11.9	0.57	5.16
OBW	24	7.2±1.15	6.7- 8.3	0.41	5.65	6	7.4±.14	7.0- 7.8	0.33	4.51
IBW	22	2.6±1.75	2.2- 3.0	0.21	8.22	6	2.6±.10	2.3- 3.0	0.25	9.69
C^1-M^4	26	6.9±1.04	6.5- 7.4	0.30	4.28	7	7.2±.06	7.0- 7.4	0.16	2.24
M^{1-4}	27	4.3± .68	4.0- 4.6	0.15	3.60	7	4.4±.04	4.3- 4.6	0.11	2.45
M^{1-3}	31	3.9± .61	3.7- 4.2	0.13	3.28	9	4.0±.03	3.9- 4.1	0.08	1.98
R-LM^3	25	6.4± .95	5.9- 7.1	0.30	4.75	7	6.6±.07	6.4- 6.9	0.19	2.83
FM	22	3.9± .93	3.5- 4.2	0.17	4.36	7	3.9±.08	3.6- 4.2	0.20	5.13
IO	25	4.3±1.14	4.0- 4.8	0.24	5.70	7	4.5±.06	4.3- 4.8	0.16	3.58
VV	26	4.5±2.04	3.6- 5.3	0.38	8.37	7	4.6±.13	4.3- 5.3	0.35	7.52
DL	28	13.9±1.49	12.6-15.7	0.85	6.10	7	14.5±.25	13.5-15.5	0.66	4.53
I_1-M_4	27	8.1± .89	7.5- 8.8	0.38	4.64	7	8.4±.05	8.3- 8.6	0.14	1.68
M_{1-4}	28	4.7± .59	4.4- 4.9	0.15	3.14	7	4.8±.02	4.8- 4.9	0.04	8.33
M_{1-3}	31	3.6± .81	3.4- 3.9	0.16	4.50	9	3.7±.03	3.6- 3.8	0.09	2.34
C-AP	26	4.1±1.57	3.7- 4.6	0.26	6.43	6	4.4±.06	4.2- 4.5	0.15	3.36
C-AR	26	4.1±1.79	3.5- 4.7	0.30	7.35	6	4.2±.12	2.9- 4.7	0.31	7.12
NL	25	7.4±1.48	6.5- 8.3	0.55	7.38	7	7.9±.12	7.4- 8.3	0.31	3.97
NW	25	2.9±1.72	2.5- 3.4	0.25	8.58	7	2.9±.06	2.6- 3.0	0.15	5.21
NWMN	25	1.3±2.22	1.1- 1.6	0.14	11.09	7	1.2±.05	1.1- 1.5	0.14	11.75
PN	25	3.0±2.34	2.3- 3.6	0.35	11.72	7	3.3±.13	2.8- 3.6	0.35	10.73
PLF-AB	22	4.3±1.00	4.0- 4.8	0.20	4.67	7	4.4±.03	4.4- 4.6	0.09	2.07
SD	24	4.9±1.05	4.4- 3.4	0.25	5.16	7	5.0±.07	5.9- 5.4	0.18	3.62
	P. m. (Townsville)					P. m.(sinualis form, N.T.)				
BL	2	18.7±.57	18.2-19.1	0.80	4.28	10	18.5±.06	17.6-19.9	0.20	1.10
ZW	2	10.9±.27	10.8-11.0	0.38	3.45	11	10.8±.12	10.1-11.4	0.39	3.57
OBW	2	7.4±.22	7.0- 7.8	0.33	4.51	11	7.6±.09	7.1- 8.0	0.30	3.95
IBW	2	2.8±.22	2.7- 2.8	0.32	11.29	11	2.8±.06	2.3- 3.1	0.21	7.46
C^1-M^4	2	6.8±.37	6.6- 7.0	0.53	7.81	11	7.1±.09	6.6- 7.6	0.29	4.06
M^{1-4}	2	4.4±.33	4.2- 4.5	0.47	10.73	11	4.3±.04	4.1- 4.5	0.14	5.35
M^{1-3}	3	4.0±.12	3.8- 4.2	0.21	5.30	11	3.9±.04	3.7- 4.1	0.12	3.13
R-LM^3	2	6.5±.27	6.4- 6.6	0.38	5.78	10	6.4±.04	6.3- 6.6	0.12	1.84
FM	2	3.9±.22	3.8- 3.9	0.32	8.11	10	3.9±.08	3.5- 4.2	0.24	6.15
IO	2	4.4±.22	4.3- 4.4	0.32	7.19	11	4.3±.08	3.9- 4.7	0.26	5.95
VV	2	4.2±.50	3.8- 4.5	0.71	16.84	11	4.5±.09	4.1- 5.0	0.31	6.96
DL	2	14.4±.33	14.2-14.5	0.47	3.28	11	14.2±.16	13.7-15.5	0.53	3.73
I_1-M_4	2	8.1±.43	7.8- 8.3	0.60	7.41	11	8.3±.11	7.7- 8.9	0.36	4.33
M_{1-4}	2	4.6±.27	4.5- 4.7	0.38	8.17	10	4.7±.07	4.4- 5.0	0.21	4.40
M_{1-3}	3	3.5±.14	3.4- 3.8	0.23	6.69	10	3.7±.06	3.3- 3.9	0.20	6.51
C-AP	2	4.3±.33	4.1- 4.4	0.47	10.98	11	4.4±.06	3.9- 4.6	0.20	4.93
C-AR	2	4.6±.33	4.4- 4.7	0.47	10.27	11	4.2±.07	3.3- 4.6	0.23	5.48
NL	2	7.8±.43	7.5- 8.0	0.60	7.69	10	7.6±.13	7.0- 8.4	0.41	5.43
NW	2	3.1±.33	2.9- 3.2	0.47	15.23	10	3.1±.07	2.8- 3.5	0.22	7.06
NWMN	2	1.5±.27	1.4- 1.6	0.38	25.07	10	1.3±.04	1.2- 1.5	0.12	9.38
PN	2	3.2±.27	3.1- 3.3	0.38	11.75	10	2.8±.06	2.4- 3.6	0.18	6.54
PLF-AB	2	4.4±.27	4.3- 4.5	0.37	8.55	10	4.6±.14	4.4- 4.8	0.43	9.41
SD	2	5.1±.22	5.0- 5.1	0.32	6.20	11	4.6±.08	4.2- 5.0	0.26	5.52

TABLE 1 (cont'd)

	N	$\bar{x} \pm \tau$	OR	s	CV	N	$\bar{x} \pm \tau$	OR	s	CV
	P. maculata (Arakun Mission)					*P. ingrami* (total)				
BL	3	17.2±.42	16.4-17.7	0.72	4.21	11	15.9±.16	14.8-17.3	0.52	3.25
ZW	3	9.9±.26	9.4-10.3	0.45	4.57	14	9.2±.20	8.4-10.9	0.76	8.26
OBW	3	7.1±.14	6.8- 7.2	0.23	3.30	14	7.0±.10	6.5- 7.9	0.39	5.59
IBW	3	2.4±.21	2.1- 2.8	0.36	15.00	12	2.4±.09	1.8- 2.9	0.32	13.53
C^1-M^4	3	6.7±.12	6.5- 6.9	0.21	3.16	15	5.9±.08	5.4- 6.5	0.31	5.30
M^{1-4}	3	4.2±.04	4.1- 4.2	0.07	1.67	15	3.6±.04	3.2- 3.8	0.16	4.45
M^{1-3}	3	3.8±0	-	-	-	16	3.3±.04	2.9- 3.5	0.16	4.94
R-LM^3	3	6.0±.12	5.8- 6.2	0.20	3.33	15	5.4±.07	4.8- 6.2	0.29	5.33
FM	3	3.8±.04	3.7- 3.8	0.07	1.84	12	3.6±.04	3.4- 3.8	0.14	3.84
IO	3	3.9±.04	3.8- 3.9	0.07	1.79	15	3.9±.06	3.4- 4.2	0.24	6.05
VV	3	4.1±.22	3.8- 4.5	0.38	9.29	14	3.7±.09	3.3- 4.6	0.35	9.57
DL	3	13.2±.25	12.7-13.5	0.44	3.30	14	11.8±.19	10.4-13.7	0.71	6.00
I_1-M_4	3	7.8±.15	7.6- 8.1	0.25	3.27	15	6.8±.07	6.3- 7.3	0.27	3.95
M_{1-4}	3	4.6±.04	4.5- 4.6	0.07	1.52	15	4.0±.04	3.7- 4.2	0.15	3.77
M_{1-3}	3	3.5±.04	3.5- 3.6	0.07	2.00	15	3.1±.04	2.7- 3.3	0.15	4.78
C-AP	3	4.0±.12	3.8- 4.2	0.20	5.00	13	3.6±.08	3.2- 4.0	0.29	7.93
C-AR	3	4.2±.12	4.0- 4.4	0.21	5.05	14	3.4±.10	2.8- 4.0	0.36	10.72
NL	2	6.7±.26	6.4- 6.9	0.36	5.31	14	6.3±.14	5.4- 7.5	0.53	8.49
NW	3	2.8±.15	2.6- 3.1	0.25	9.10	14	2.9±.09	2.3- 3.5	0.32	11.07
NWMN	2	1.4±.07	1.3- 1.4	0.10	7.14	14	1.3±.04	1.0- 1.5	0.15	11.87
PN	2	2.9±.07	2.8- 2.9	0.10	3.45	14	2.2±.10	1.7- 2.8	0.36	16.39
PLF-AB	3	4.1±.15	3.8- 4.3	0.25	6.22	13	4.5±.05	4.1- 4.7	0.19	4.16
SD	3	4.5±.10	4.3- 4.6	0.17	3.84	13	3.5±.08	3.2- 4.2	0.30	8.61

	N	$\bar{x} \pm \tau$	OR	s	CV	N	$\bar{x} \pm \tau$	OR	s	CV
	P. i. (Richmond)					*P. i.* (Normanton)				
BL	4	15.9±.20	15.4-17.1	0.40	2.49	3	16.1±.67	15.0-17.3	1.15	9.40
ZW	5	9.0±.21	8.5- 9.8	0.47	5.27	4	9.8±.57	8.4-10.9	1.14	11.65
OBW	5	7.1±.12	6.8- 7.4	0.28	3.92	4	7.2±.34	6.5- 7.9	0.68	9.45
IBW	5	2.2±.14	1.8- 2.6	0.31	14.00	3	2.7±.17	2.4- 2.9	0.29	10.80
C^1-M^4	5	5.9±.06	5.7- 6.0	0.14	2.39	4	6.2±.13	5.9- 6.5	0.25	4.06
M^{1-4}	5	3.6±.17	3.4- 3.7	0.39	10.75	4	3.8±.04	3.7- 3.8	0.08	2.14
M^{1-3}	5	3.3±.05	3.1- 3.4	0.11	3.39	4	3.4±.06	3.3- 3.5	0.10	2.94
R-LM^3	5	5.4±.09	3.1- 5.6	0.21	3.93	4	5.7±.16	3.2- 6.2	0.31	5.48
FM	4	3.8±.03	3.7- 3.8	0.06	1.50	3	3.6±.04	3.5- 3.6	0.07	1.94
IO	5	3.8±.06	3.7- 4.0	0.13	3.48	4	3.9±.20	3.4- 4.2	0.40	10.51
VV	4	3.7±.12	3.4- 3.9	0.24	6.59	4	4.0±.24	3.6- 4.6	0.49	12.23
DL	4	11.9±.30	11.4-12.8	0.61	5.11	4	12.4±.68	10.9-13.7	1.36	11.01
I_1-M_4	5	6.9±.09	6.6- 7.1	0.20	2.90	4	7.1±.20	6.7- 7.3	0.41	5.74
M_{1-4}	5	4.0±.03	3.9- 4.0	0.07	1.75	4	4.2±.04	4.1- 4.2	0.08	1.93
M_{1-3}	5	3.0±.03	3.0- 3.1	0.07	2.33	4	3.2±.04	3.1- 3.3	0.08	2.54
C-AP	3	3.6±.06	3.5- 3.7	0.10	2.78	4	3.8±.13	3.4- 4.0	0.26	6.96
C-AR	4	3.4±.22	3.1- 4.0	0.44	12.93	4	3.7±.16	3.3- 4.0	0.31	8.40
NL	4	6.3±.18	5.9- 6.6	0.36	5.70	4	6.8±.12	6.3- 7.5	0.24	3.59
NW	4	2.9±.13	2.6- 3.2	0.25	8.67	4	3.0±.28	2.3- 3.5	0.57	18.83
NWMN	4	1.2±.05	1.1- 1.3	0.10	8.33	4	1.2±.10	1.0- 1.5	0.21	17.33
PN	4	2.3±.11	2.0- 2.5	0.22	9.72	4	2.5±.17	2.0- 2.8	0.34	13.66
PLF-AB	4	4.6±.05	4.5- 4.7	0.10	2.17	4	4.4±.09	4.2- 4.6	0.18	4.15
SD	4	3.4±.10	3.2- 3.7	0.21	6.12	4	3.8±.19	3.3- 4.2	0.37	9.84

	N	$\bar{x} \pm \tau$	OR	s	CV	N	$\bar{x} \pm \tau$	OR	s	CV
	P. i. (201 km W. of Burketown)					*P. i.* (owl pellet, Barkly Tbld)				
BL	2	15.4±.45	14.8-15.9	0.78	5.07					
ZW	3	8.8±.21	8.5- 9.2	0.36	4.10					
OBW	3	6.9±.10	6.8- 7.1	0.17	2.51					
IBW	2	2.1±0	2.2- 2.2	-	-					
C^1-M^4	3	5.5±.14	5.4- 5.8	0.23	4.26	8	5.4±.08	5.3- 5.6	0.11	2.09
M^{1-4}	3	3.4±.12	3.2- 3.6	0.21	6.24	8	3.4±.04	3.3- 3.6	0.11	3.32
M^{1-3}	3	3.1±.12	2.9- 3.3	0.20	6.45	8	3.1±.05	2.9- 3.3	0.13	4.22
R-LM^3	3	5.2±.09	3.1- 5.4	0.16	3.04					
FM	3	3.6±.09	3.4- 3.7	0.16	4.39					
IO	3	3.8±.10	3.7- 4.0	0.17	4.55					
VV	3	3.4±.07	3.3- 3.5	0.12	3.60	5	3.5±.09	3.3- 3.8	0.20	5.71
DL	3	11.2±.26	10.7-11.6	0.46	4.09	15	10.9±.08	10.5-11.5	0.31	2.89
I_1-M_4	3	6.5±.12	6.3- 6.7	0.20	3.08	15	6.2±.05	6.0- 6.6	0.18	2.83
M_{1-4}	3	3.9±.09	3.7- 4.0	0.16	4.05	16	3.7±.04	3.6- 4.1	0.15	4.00
M_{1-3}	3	2.9±.12	2.7- 3.1	0.20	6.90	16	2.9±.02	2.8- 3.1	0.10	3.32
C-AP	3	3.5±.04	3.5- 3.6	0.07	2.00	13	3.3±.04	3.0- 3.5	0.16	4.87
C-AR	3	3.3±.04	3.2- 3.3	0.07	2.12	17	3.1±.04	2.8- 3.4	0.18	4.42
NL	3	5.8±.07	5.7- 5.9	0.12	2.11					
NW	3	2.9±.04	2.9- 3.0	0.07	2.41					
NWMN	3	1.2±.04	1.2- 1.3	0.07	3.83					
PN	3	1.9±.07	1.8- 2.0	0.12	6.42					
PLF-AB	3	4.4±.17	4.1- 4.7	0.30	6.81					
SD	3	3.3±.07	3.2- 3.4	0.12	3.70					

TABLE 1 (cont'd)

	P. tenuirostris					*P. gilesi*				
	N	$\bar{x} \pm \sigma$	OR	s	CV	N	$\bar{x} \pm \sigma$	OR	s	CV
BL	8	16.3±.27	15.2-17.4	0.76	4.67	4	18.4±.65	16.6-19.4	1.31	7.11
ZW	8	8.7±.13	8.3- 9.3	0.36	4.10	3	10.6±.64	9.5-11.7	1.10	10.40
OBW	9	6.5±.09	6.2- 6.9	0.27	4.11	4	7.6±.23	6.9- 8.0	0.47	6.17
IBW	9	2.3±.05	2.1- 2.5	0.15	6.70	4	2.8±.05	2.7- 2.9	0.10	3.57
C^1–M^4	12	6.1±.06	5.8- 6.3	0.20	3.24	5	7.0±.24	6.2- 7.6	0.53	7.56
M^{1-4}	12	3.7±.04	3.4- 3.8	0.15	4.00	5	4.4±.14	4.0- 4.8	0.30	6.91
M^{1-3}	12	3.3±.03	3.1- 3.5	0.12	3.65	5	3.9±.13	3.5- 4.3	0.29	7.36
R–LM^3	11	5.5±.06	5.2- 5.8	0.19	3.40	5	6.4±.18	5.7- 6.7	0.40	6.20
FM	7	3.6±.05	3.5- 3.8	0.13	3.58	4	3.8±.07	3.7- 4.0	0.15	3.97
IO	11	3.7±.04	3.5- 4.0	0.14	3.70	5	4.3±.07	4.1- 4.5	0.16	3.67
VV	9	3.9±.08	3.5- 4.2	0.23	5.87	5	4.4±.18	4.0- 4.9	0.39	8.95
DL	12	12.2±.13	11.4-13.0	0.45	3.71	5	14.1±.40	12.7-15.0	0.89	6.33
I_1-M_4	12	7.1±.08	6.6- 7.4	0.28	4.01	5	8.2±.14	7.7- 8.9	0.31	3.81
M_{1-4}	13	4.1±.07	3.8- 4.8	0.25	6.06	5	4.7±.16	4.3- 5.1	0.36	7.74
M_{1-3}	13	3.1±.04	2.9- 3.8	0.15	4.75	5	3.6±.11	3.3- 3.9	0.24	5.95
C-AP	11	3.5±.03	3.3- 3.7	0.11	3.11	4	4.1±.18	3.6- 4.3	0.35	8.55
C-AR	12	3.4±.06	3.1- 3.7	0.21	6.08	5	4.0±.13	3.7- 4.4	0.30	7.50
NL	11	6.7±.16	5.8- 7.6	0.54	8.06	5	7.7±.23	6.9- 8.3	0.50	6.56
NW	7	2.7±.09	2.4- 3.2	0.23	8.60	5	3.2±.06	3.0- 3.4	0.14	4.41
NWMN	10	1.0±.05	0.8- 1.2	0.15	14.53	4	1.4±.12	1.0- 1.5	0.24	17.49
PN	10	2.4±.06	2.1- 2.7	0.19	7.97	3	2.9±.14	2.8- 3.2	0.23	8.07
PLF-AB	10	4.2±.08	3.7- 4.5	0.24	5.66	4	4.8±.10	4.5- 4.9	0.20	4.17
SD	10	3.9±.07	3.6- 4.1	0.21	5.27	4	3.9±.04	3.8- 4.0	0.09	2.21

	P. i. (*subtilissima* form)
BL	15.5
ZW	8.8
OBW	6.8
IBW	2.2
C^1–M^4	5.8
M^{1-4}	2.5
M^{1-3}	3.2
R–LM^3	5.2
FM	3.5
IO	4.1
VV	3.7
DL	11.6
I_1-M_4	6.8
M_{1-4}	4.0
M_{1-3}	3.1
C-AP	3.5
C-AR	3.3
NL	6.2
NW	2.9
NWMN	1.3
PN	1.7
PLF-AB	4.4
SD	3.5

	N	$\bar{x} \pm \sigma$	OR	s	CV
	P. i. (fossil Kimberleys)				
DL	7	10.6±.12	10.2-11.1	0.32	3.06
I_1-M_4	8	5.9±.10	5.4- 6.3	0.28	4.78
M_{1-4}	9	3.7±.05	3.4- 3.8	0.15	4.05
M_{1-3}	4	2.8±.05	2.7- 2.9	0.10	3.57
C-AP	6	3.4±.05	3.2- 3.5	0.13	3.94
C-AR	6	3.1±.07	2.9- 3.3	0.17	5.39

	P. i. brunneus Holotype
ZW	8.9
OBW	6.8
IBW	1.8
C^1–M^4	5.7
M^{1-4}	3.4
M^{1-3}	3.1
R–LM^3	5.1
FM	
IO	3.7
VV	
DL	11.7
I_1-M_4	6.6
M_{1-4}	3.9
M_{1-3}	3.0
C-AP	3.5
C-AR	3.1

	P. t. Holotype
OBW	6.8
IBW	2.5
C^1–M^4	6.0
M^{1-4}	3.5
M^{1-3}	3.2
R–LM^3	5.5
FM	
IO	
VV	3.5
DL	12.3
I_1-M_4	6.6
M_{1-4}	3.9
M_{1-3}	3.0
C-AP	3.5
C-AR	3.5

TABLE 2: RATIOS OF CRANIAL, DENTAL AND EXTERNAL CHARACTERS IN *Planigale*

Locality names have been abbreviated as follows: Mt Molloy, Qd: Townsville, Qd; Humpty Doo, N.T.; Aurukun Mission, Qd; Richmond, Qd; Karumba, Qd; 200 km west of Burketown in N.T.; Brunette Downs, N.T.; fossil Kimberleys sample from surface of cave in southern Kimberleys. X, sample mean; N, sample number; O.R., observed range; TV, tail-vent length; HB, head-body length (nose to vent); HF, hind-foot length; ST, length of supratragus of ear; E, ear (tip of pinna to notch). Other abbreviations as in Table 1.

		BL/ZW	IO/ZW	BW/ZW	BW/$\overline{M^{1-3}}$	BL/$\overline{M^{1-3}}$	SD/ZW	SD/BL	SD/C^1-M^4	SD/IO	FM/SD	FM/ZW	$\overline{M^{1-3}}$/ZW
Planigale novaeguineae All	$\bar{x}$(N)	1.74 (2)	0.41 (2)	0.40 (2)	1.13 (2)	1.09 (2)	0.49 (2)	0.28 (2)	0.72 (2)	1.23 (2)	0.70 (2)	0.35 (2)	0.36 (2)
	O.R.	1.73-1.74	0.36-0.45	0.38-0.41	1.12-1.14	1.07-1.10	0.48-0.49	0.28	0.71-0.73	1.12-1.34	0.71-0.73	0.34-0.36	0.34-0.37
P. maculata All	$\bar{x}$(N)	1.73 (31)	0.40 (34)	0.44 (32)	1.20 (32)	1.13 (31)	0.45 (34)	0.26 (31)	0.70 (34)	1.13 (33)	0.80 (31)	0.36 (31)	0.37 (35)
	O.R.	1.60-1.80	0.35-0.44	0.41-0.49	1.05-1.34	1.03-1.24	0.41-0.51	0.23-0.28	0.59-0.78	0.96-1.34	0.70-1.00	0.32-0.41	0.33-0.42
P. maculata All Queensland	$\bar{x}$(N)	1.73 (22)	0.40 (24)	0.44 (22)	1.18 (22)	1.10 (22)	0.47 (24)	0.27 (22)	0.72 (24)	1.16 (23)	0.78 (22)	0.36 (22)	0.37 (25)
	O.R.	1.60-1.80	0.35-0.44	0.41-0.48	1.05-1.37	1.03-1.16	0.42-0.51	0.25-0.28	0.66-0.78	0.96-1.34	0.70-0.89	0.32-0.41	0.33-0.42
P. maculata Mt. Molloy	$\bar{x}$(N)	1.72 (7)	0.41 (7)	0.43 (6)	1.20 (6)	1.11 (7)	0.46 (7)	0.27 (7)	0.70 (7)	1.12 (7)	0.78 (7)	0.35 (7)	0.37 (7)
	O.R.	1.68-1.77	0.38-0.43	0.41-0.46	1.15-1.28	1.07-1.15	0.44-0.48	0.26-0.27	0.67-0.73	1.09-1.18	0.70-0.86	0.32-0.41	0.34-0.40
P. maculata Townsville	$\bar{x}$(N)	1.72 (2)	0.40 (2)	0.43 (2)	1.17 (2)	1.13 (2)	0.46 (2)	0.28 (2)	0.76 (2)	1.16 (2)	0.77 (2)	0.36 (2)	0.36 (2)
	O.R.	1.69-1.74	0.40	0.42-0.43	1.15-1.18	1.13	0.46	0.28	0.76	1.16	0.77	0.35-0.36	0.35-0.37
P. maculata All N. Territory	$\bar{x}$(N)	1.72 (9)	0.40 (10)	0.45 (10)	1.24 (10)	1.19 (9)	0.43 (10)	0.25 (9)	0.65 (10)	1.07 (10)	0.85 (9)	0.36 (9)	0.36 (10)
	O.R.	1.65-1.80	0.35-0.44	0.41-0.49	1.05-1.33	1.13-1.24	0.41-0.47	0.23-0.26	0.59-0.68	0.96-1.15	0.75-1.00	0.32-0.42	0.33-0.41
P. maculata Humpty Doo	$\bar{x}$(N)	1.73 (5)	0.42 (6)	0.45 (6)	1.22 (6)	1.17 (5)	0.43 (6)	0.24 (5)	0.65 (6)	1.05 (6)	0.89 (5)	0.38 (5)	0.37 (6)
	O.R.	1.65-1.80	0.38-0.44	0.43-0.46	1.05-1.33	1.13-1.21	0.41-0.45	0.23-0.25	0.59-0.68	0.96-1.14	0.78-1.00	0.36-0.42	0.35-0.41
P. maculata Arakun	$\bar{x}$(N)	1.75 (3)	0.39 (3)	0.47 (3)	1.23 (3)	1.07 (3)	0.46 (3)	0.26 (3)	0.67 (3)	1.16 (3)	0.84 (3)	0.38 (3)	0.38 (3)
	O.R.	1.71-1.79	0.38-0.40	0.43-0.51	1.16-1.34	1.00-1.13	0.45-0.47	0.26	0.66-0.70	1.13-1.18	0.83-0.86	0.31-0.39	0.37-0.40
P. tenuirostris All	$\bar{x}$(N)	1.87 (8)	0.43 (8)	0.48 (8)	1.26 (9)	1.27 (10)	0.44 (8)	0.24 (8)	0.64 (10)	1.03 (9)	0.95 (7)	0.42 (7)	0.39 (8)
	O.R.	1.76-1.98	0.43-0.45	0.45-0.51	1.18-1.34	1.18-1.34	0.43-0.46	0.22-0.25	0.59-0.69	0.95-1.08	0.85-1.03	0.38-0.45	0.36-0.41
P. ingrami All	$\bar{x}$(N)	1.72 (9)	0.42 (11)	0.50 (11)	1.44 (11)	1.37 (11)	0.38 (11)	0.22 (9)	0.60 (11)	0.91 (11)	1.06 (10)	0.40 (10)	0.35 (12)
	O.R.	1.65-1.84	0.39-0.44	0.44-0.56	1.30-1.61	1.24-1.52	0.36-0.40	0.21-0.23	0.53-0.65	0.85-1.00	0.95-1.16	0.34-0.45	0.32-0.40
P. ingrami Richmond	$\bar{x}$(N)	1.76 (4)	0.43 (4)	0.53 (5)	1.48 (5)	1.37 (4)	0.38 (4)	0.22 (4)	0.58 (4)	0.89 (4)	1.11 (4)	0.42 (4)	0.37 (5)
	O.R.	1.71-1.84	0.40-0.44	0.50-0.56	1.38-1.61	1.35-1.42	0.36-0.40	0.21-0.22	0.59-0.62	0.84-0.95	1.03-1.16	0.39-0.45	0.34-0.40
P. ingrami Karumba	$\bar{x}$(N)	1.69 (2)	0.40 (3)	0.46 (3)	1.37 (3)	1.31 (3)	0.38 (3)	0.23 (2)	0.62 (3)	0.97 (3)	0.95 (2)	0.37 (2)	0.33 (3)
	O.R.	1.65-1.72	0.39-0.40	0.45-0.46	1.30-1.43	1.30-1.32	0.36-0.40	0.22-0.23	0.61-0.65	0.91-1.00	0.95	0.34-0.38	0.32-0.36
P. ingrami Burketown	$\bar{x}$(N)	1.72 (2)	0.44 (3)	0.53 (2)	1.49 (2)	1.43 (3)	0.37 (3)	0.22 (2)	0.59 (3)	0.86 (3)	1.10 (3)	0.41 (3)	0.35 (3)
	O.R.	1.70-1.73	0.43-0.44	0.53	1.39-1.58	1.24-1.52	0.37-0.38	0.21-0.22	0.59	0.85-0.87	1.00-1.16	0.37-0.43	0.34-0.38
P. ingrami Brunette Downs	$\bar{x}$(N)	-	-	-	-	-	-	-	-	-	-	-	-
	O.R.	-	-	-	-	-	-	-	-	-	-	-	-
P. ingrami Kimberleys	$\bar{x}$(N)	1.76 (1)	0.47 (1)	0.52 (1)	1.44 (1)	1.38 (1)	0.40 (1)	0.23 (1)	0.60 (1)	0.85 (1)	1.00 (1)	0.40 (1)	0.36 (1)
	O.R.	1.76	0.47	0.52	1.44	1.38	0.40	0.23	0.60	0.85	1.00	0.40	0.36
P. ingrami Fossil, Kimberleys	$\bar{x}$(N)	-	-	-	-	-	-	-	-	-	-	-	-
	O.R.	-	-	-	-	-	-	-	-	-	-	-	-
P. gilesi All	$\bar{x}$(N)	1.73 (4)	0.40 (4)	0.45 (4)	1.22 (4)	1.23 (4)	0.37 (4)	0.22 (4)	0.57 (4)	0.94 (4)	0.98 (4)	0.36 (4)	0.37 (4)
	O.R.	1.66-1.80	0.37-0.43	0.41-0.50	1.14-1.28	1.14-1.29	0.34-0.40	0.21-0.23	0.53-0.61	0.91-0.98	0.93-1.03	0.32-0.41	0.33-0.40
WAM3432 Tambrey, W.A.		1.69	.39	.42	1.32	-	0.40	0.24	0.65	1.02	0.93	0.37	0.32

		$\frac{C^1-P^1}{M^{1-3}}$	$\frac{I_1-P_4}{M_{1-3}}$	NL/BL	NW/ZW	NW/NL	PN/NL	VV/BL	DL/BL	TV/HB	HF/HB	ST/E
Planigale novaeguineae All	$\bar{x}$(N)	0.82 (2)	1.05 (2)	0.42 (2)	0.31 (2)	0.43 (2)	0.39 (2)	0.26 (2)	0.78 (2)	0.86 (4)	0.14 (3)	-
	O.R.	0.79-0.84	1.03-1.07	0.42	0.30-0.32	0.41-0.44	0.36-0.41	0.24-0.28	0.77-0.79	0.84-0.87	0.14-0.15	-
P. maculata All	$\bar{x}$(N)	0.69 (36)	0.96 (36)	0.41 (31)	0.28 (34)	0.40 (34)	0.41 (33)	0.25 (31)	0.77 (31)	0.85 (15)	0.17 (15)	0.32 (5)
	O.R.	0.61-0.82	0.78-1.09	0.38-0.44	0.25-0.33	0.34-0.45	0.32-0.48	0.21-0.29	0.74-0.84	0.70-1.04	0.14-0.20	0.27-0.36
P. maculata All Queensland	$\bar{x}$(N)	0.67 (26)	0.95 (27)	0.41 (22)	0.28 (25)	0.40 (25)	0.41 (25)	0.25 (22)	0.77 (22)	0.82 (13)	0.17 (13)	0.32 (5)
	O.R.	0.61-0.82	0.78-1.07	0.39-0.44	0.25-0.33	0.34-0.45	0.34-0.47	0.21-0.29	0.74-0.84	0.70-0.90	0.14-0.20	0.27-0.36
P. maculata Mt. Molloy,	$\bar{x}$(N)	0.68 (7)	0.98 (7)	0.42 (7)	0.26 (7)	0.36 (7)	0.41 (7)	0.25 (7)	0.76 (7)	0.82 (5)	0.17 (5)	0.34 (2)
	O.R.	0.61-0.73	0.92-1.05	0.41-0.43	0.25-0.28	0.35-0.38	0.35-0.47	0.23-0.29	0.75-0.77	0.70-0.90	0.16-0.19	0.33-0.35
P. maculata Townsville	$\bar{x}$(N)	0.62 (2)	0.97 (2)	0.42 (2)	0.28 (2)	0.40 (2)	0.41 (2)	0.21 (2)	0.78 (2)	0.75 (1)	0.14 (1)	-
	O.R.	0.61-0.63	0.97	0.39-0.44	0.27-0.29	0.36-0.43	0.41	0.21	0.78	0.75	0.14	-
P. maculata All N. Territory	$\bar{x}$(N)	0.73 (10)	0.98 (9)	0.41 (9)	0.29 (9)	0.41 (9)	0.41 (8)	0.24 (9)	0.77 (9)	1.04 (2)	0.16 (2)	-
	O.R.	0.63-0.80	0.87-1.09	0.38-0.43	0.26-0.33	0.38-0.44	0.32-0.48	0.22-0.25	0.75-0.78	1.04	0.15-0.16	-
P. maculata Humpty Doo	$\bar{x}$(N)	0.73 (6)	0.96 (5)	0.41 (5)	0.30 (5)	0.41 (5)	0.43 (4)	0.24 (5)	0.77 (5)	1.04 (1)	0.15 (1)	-
	O.R.	0.63-0.80	0.87-1.08	0.40-0.43	0.28-0.33	0.38-0.43	0.33-0.48	0.23-0.25	0.75-0.78	1.04	0.15	-
P. maculata Arakun	$\bar{x}$(N)	0.66 (3)	0.92 (3)	0.39 (2)	0.29 (3)	0.45 (2)	0.43 (2)	0.23 (3)	0.77 (3)	0.77 (4)	0.16 (4)	0.28 (3)
	O.R.	0.63-0.71	0.83-1.00	0.39	0.26-0.30	0.44-0.45	0.41-0.45	0.22-0.25	0.76-0.77	0.71-0.82	0.14-0.17	0.26-0.30
P. tenuirostris All	$\bar{x}$(N)	0.72 (12)	1.01 (12)	0.41 (8)	0.32 (8)	0.41 (11)	0.35 (10)	0.23 (8)	0.75 (8)	0.87 (4)	0.17 (4)	0.28 (4)
	O.R.	0.67-0.78	0.87-1.13	0.38-0.46	0.29-0.36	0.36-0.45	0.31-0.42	0.21-0.24	0.73-0.76	0.78-0.95	0.15-0.19	0.26-0.30
P. ingrami All	$\bar{x}$(N)	0.69 (20)	0.87 (27)	0.39 (9)	0.32 (11)	0.47 (11)	0.36 (11)	0.23 (9)	0.75 (9)	1.05 (8)	0.15 (6)	0.35 (3)
	O.R.	0.55-0.77	0.77-1.03	0.37-0.42	0.28-0.34	0.43-0.51	0.31-0.41	0.20-0.25	0.73-0.76	0.90-1.13	0.12-0.18	0.31-0.38
P. ingrami Richmond	$\bar{x}$(N)	0.70 (5)	0.95 (5)	0.40 (4)	0.32 (4)	0.46 (4)	0.37 (4)	0.23 (4)	0.75 (3)	1.06 (2)	0.18 (2)	-
	O.R.	0.65-0.73	0.90-1.03	0.38-0.42	0.31-0.33	0.43-0.49	0.34-0.38	0.20-0.25	0.73-0.76	1.00-1.11	0.17-0.18	-
P. ingrami Karumba	$\bar{x}$(N)	0.75 (3)	0.93 (3)	0.40 (2)	0.31 (3)	0.46 (3)	0.39 (3)	0.24 (2)	0.76 (2)	1.00 (3)	0.13 (3)	0.35 (3)
	O.R.	0.73-0.77	0.89-0.97	0.39-0.40	0.28-0.33	0.41-0.51	0.35-0.41	0.23-0.24	0.75-0.76	0.90-1.12	0.12-0.15	0.33-0.38
P. ingrami Burketown	$\bar{x}$(N)	0.68 (3)	0.91 (3)	0.38 (2)	0.33 (3)	0.50 (3)	0.32 (3)	0.22 (2)	0.75 (2)	1.10 (3)	0.16 (3)	0.33 (3)
	O.R.	0.55-0.76	0.87-0.96	0.37-0.39	0.33-0.34	0.49-0.51	0.31-0.34	0.22	0.73-0.76	1.07-1.13	0.15-0.17	0.31-0.35
P. ingrami Brunette Downs	$\bar{x}$(N)	0.66 (8)	0.87 (15)	-	-	-	-	-	-	-	-	-
	O.R.	0.58-0.73	0.77-0.93	-	-	-	-	-	-	-	-	-
P. ingrami Kimberleys	$\bar{x}$(N)	0.72 (1)	0.90 (1)	0.40 (1)	0.33 (1)	0.47 (1)	0.27 (1)	0.24 (1)	0.75 (1)	1.12 (2)	0.18 (2)	0.38 (2)
	O.R.	0.72	0.90	0.40	0.33	0.47	0.27	0.24	0.75	1.06-1.18	0.17-0.18	0.36-0.39
P. ingrami Fossil, Kimberleys	$\bar{x}$(N)	-	0.79 (9)	-	-	-	-	-	-	-	-	-
	O.R.	-	0.75-0.90	-	-	-	-	-	-	-	-	-
P. gilesi All	$\bar{x}$(N)	0.66 (5)	0.95 (5)	0.42 (4)	0.30 (4)	0.42 (5)	0.39 (4)	0.25 (4)	0.77 (4)	0.94 (6)	0.15 (7)	0.36 (4)
	O.R.	0.63-0.71	0.89-1.03	0.40-0.43	0.27-0.32	0.39-0.45	0.36-0.41	0.22-0.27	0.76-0.77	0.77-1.02	0.14-0.17	0.33-0.38
WAM3432 Tambrey, W.A.		0.82	0.74	0.40	0.32	0.47	0.34	0.22	0.97	-	-	-

PLATE 43

A–D, *Planigale maculata* (typical form). J16477, adult, Mt Molloy, Qd. A, × 5·1. B–D, × 3·7.

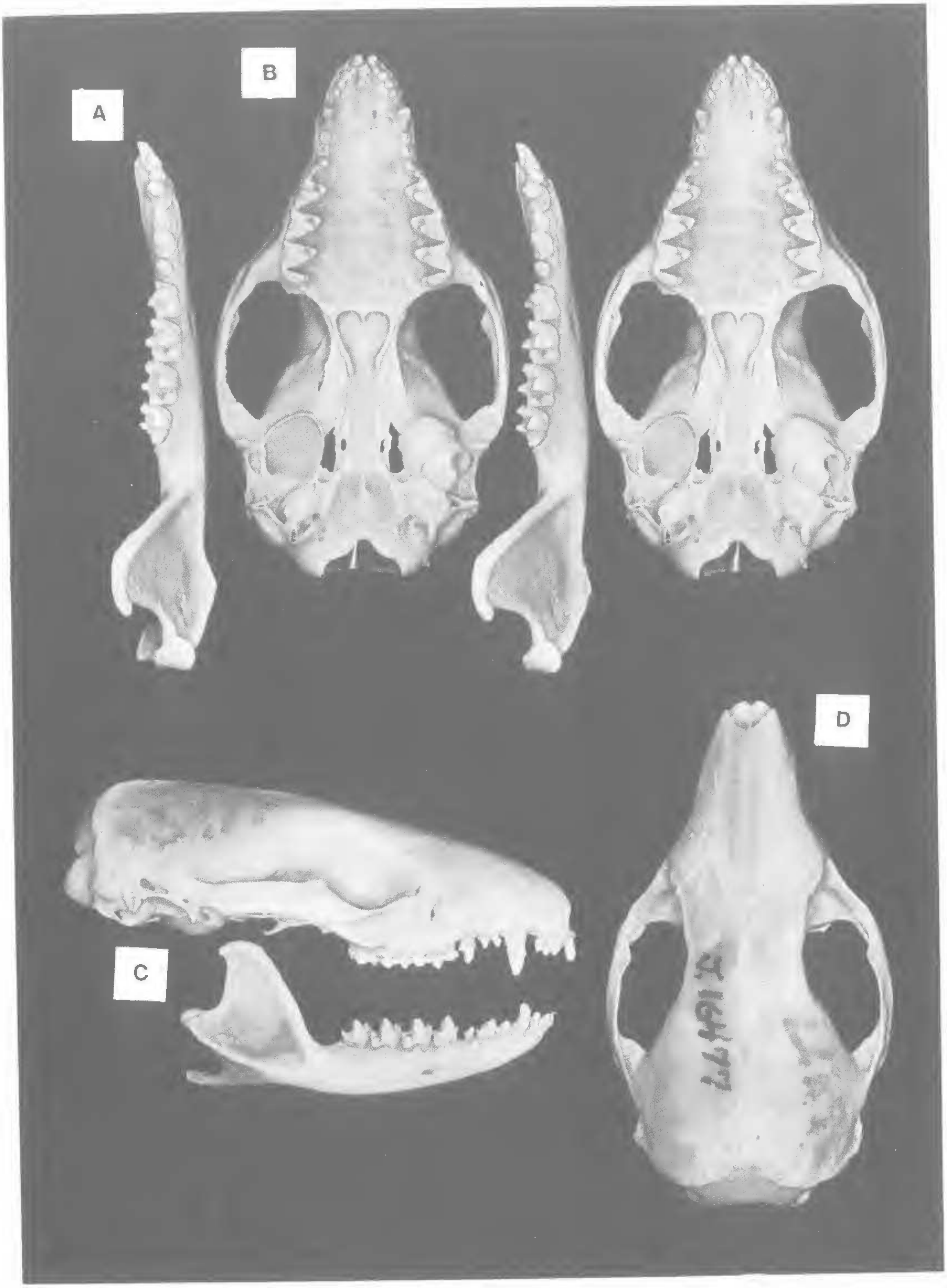

A
B
C
D
J.16477

PLATE 44

A–D, *Planigale maculata* (*sinualis* form). WAM M8095, adult, Humpty Doo, N.T. A, × 5·6. B–D, × 3·8.

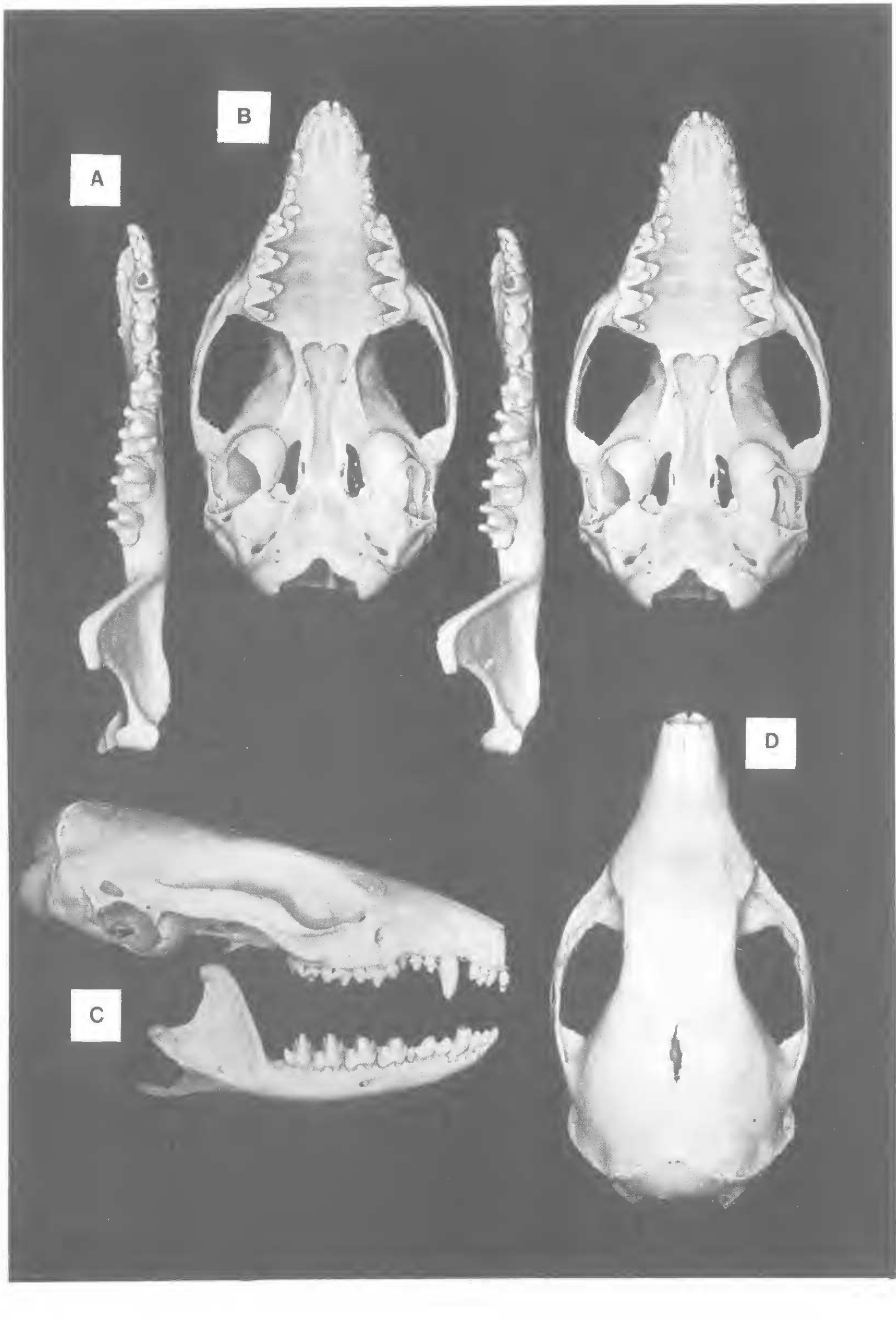

A
B
C
D

PLATE 45

A–D, *Planigale novaeguineae*. J4368, adult, New Guinea. A, × 4·6. B–D, × 3·6.

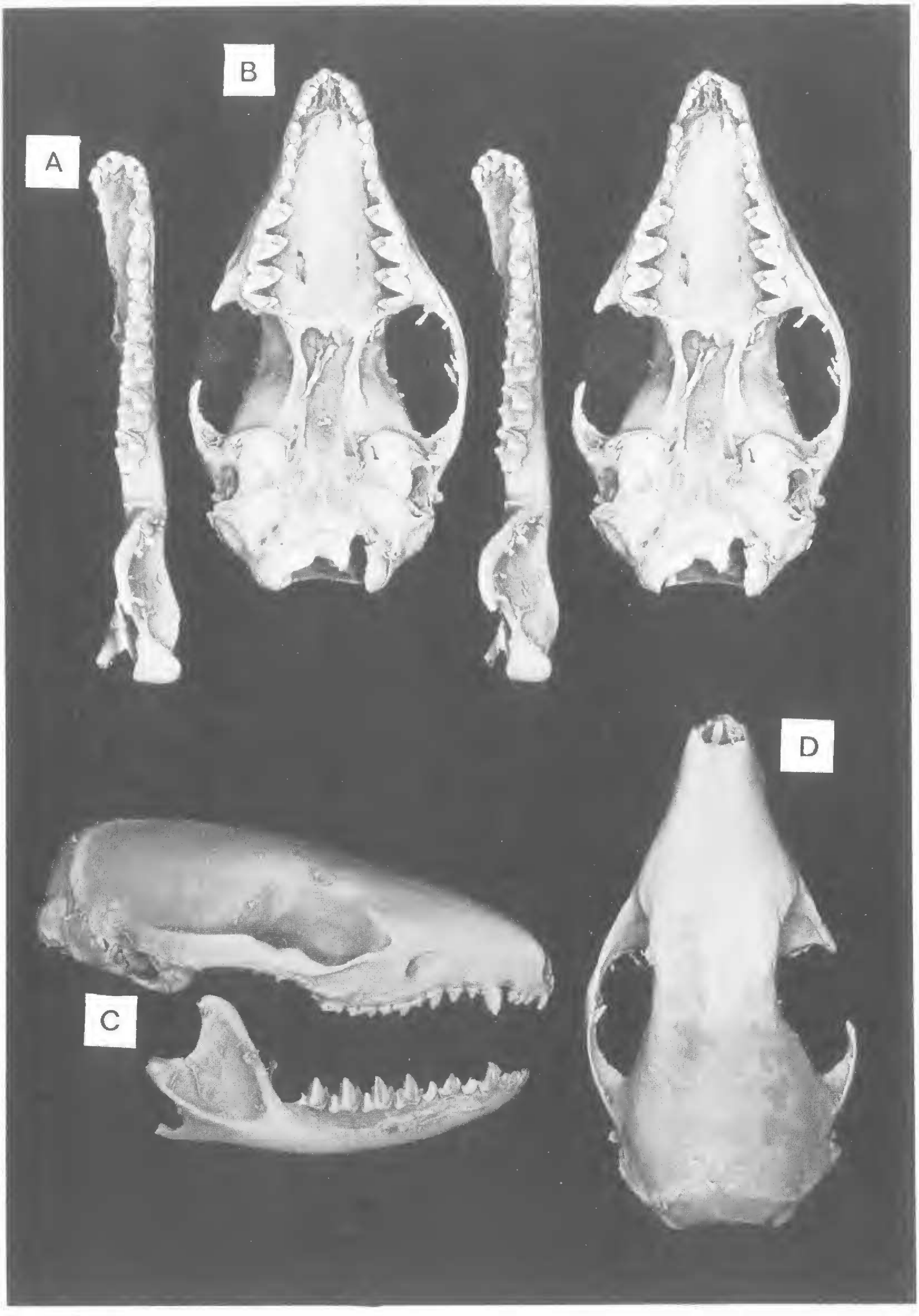

A
B
C
D

PLATE 46

A–D, *Planigale ingrami* (typical form), JM824, adult, nr Richmond, Qd. A, × 6·8. B–D, × 4·7.

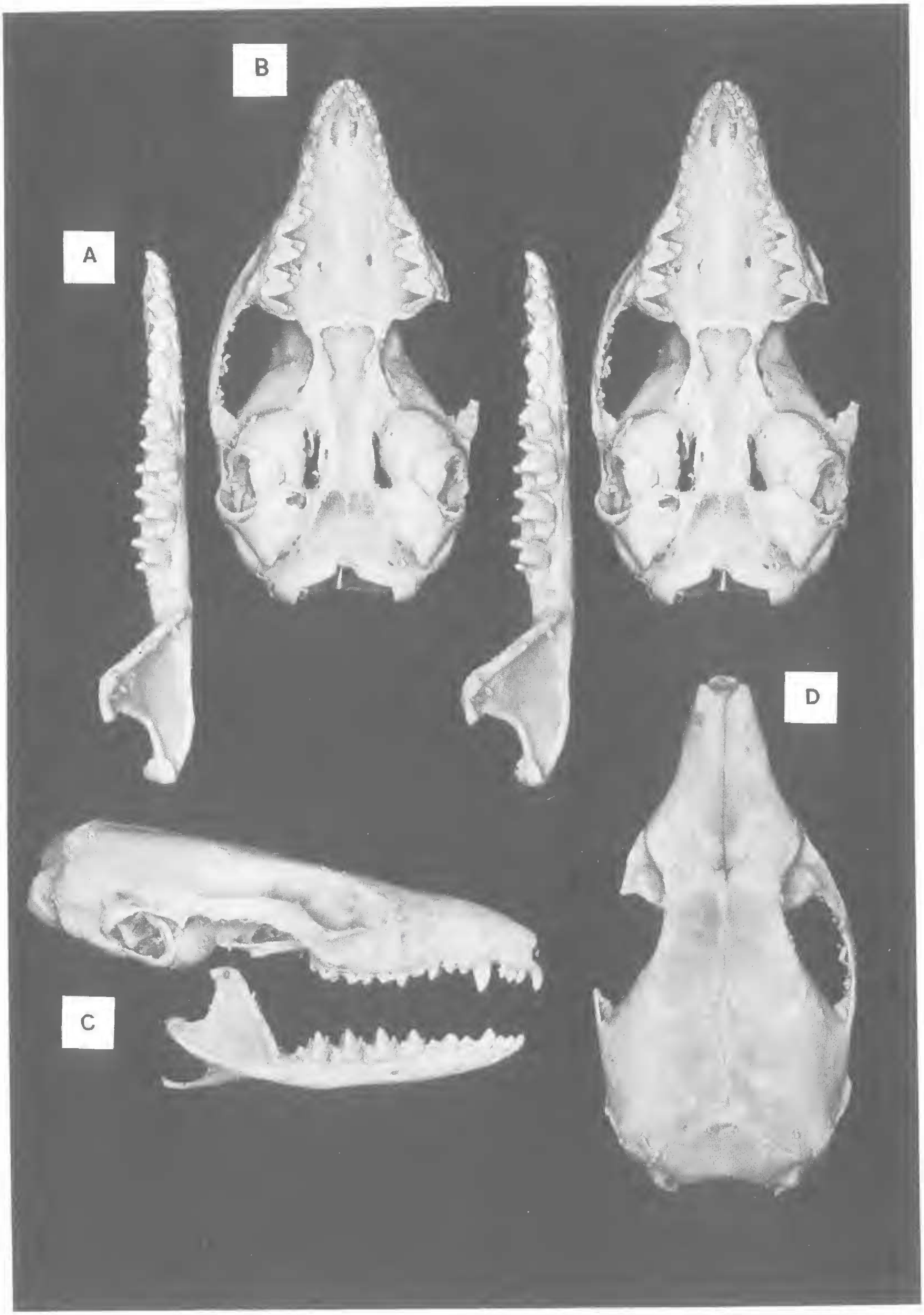

B
A
D
C

PLATE 47

A–D, *Planigale ingrami* (*subtilissima* form). WAM M2846, Ord River area, W.A. A, × 6·8. B–D, × 4·7.

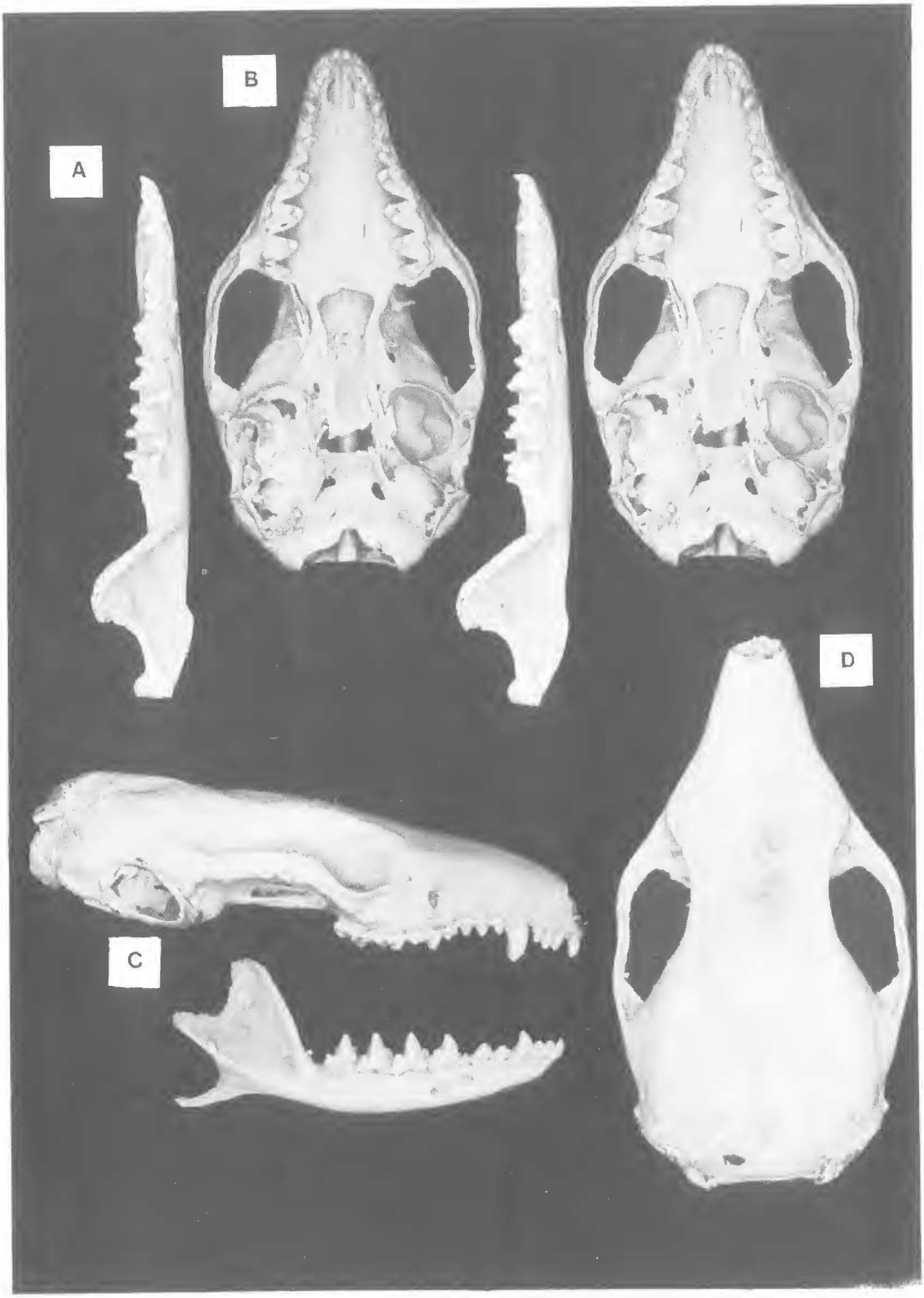

A
B
C
D

PLATE 48

A–D, *Planigale tenuirostris*. J3096, adult, Pittsworth, Qd. A, × 6·2. B–D, × 4·1.

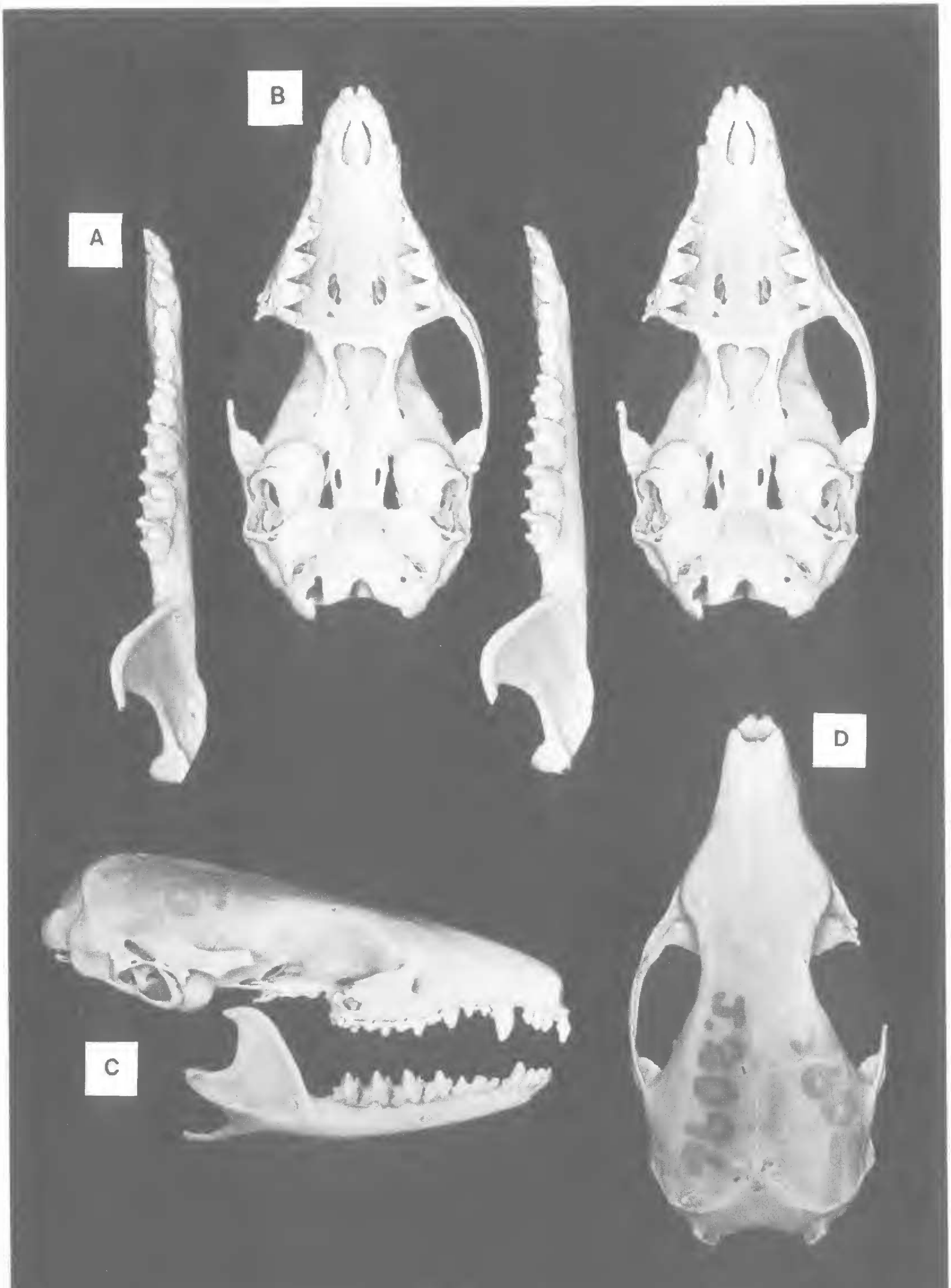

B
A
D
C

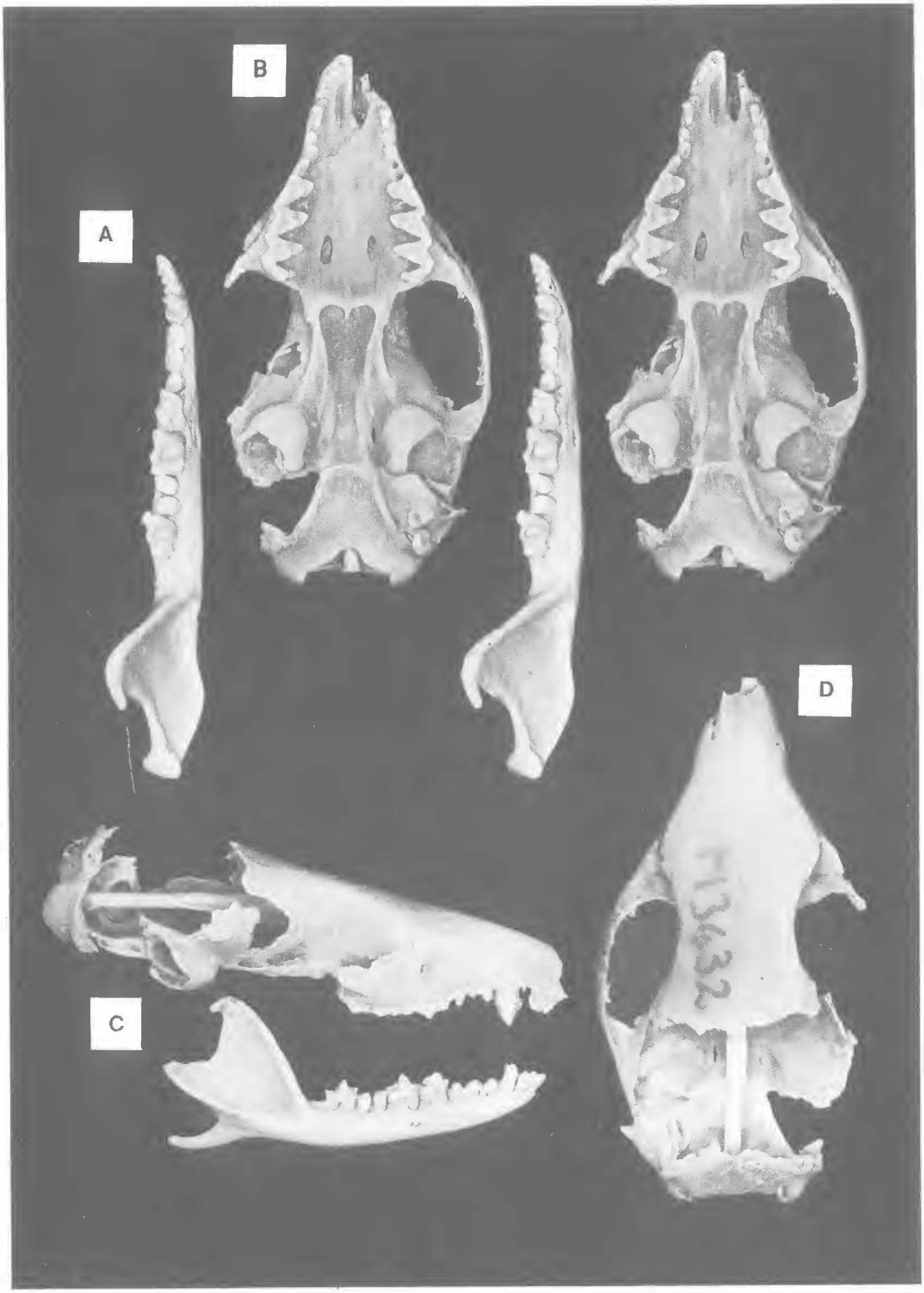
PLATE 49

A–D, *Planigale gilesi*. J21973, adult, Durrie Stn, nr Birdsville, Qd. A, × 5·9. B–D, × 4·4.


A
B
C
D

PLATE 5[illegible]

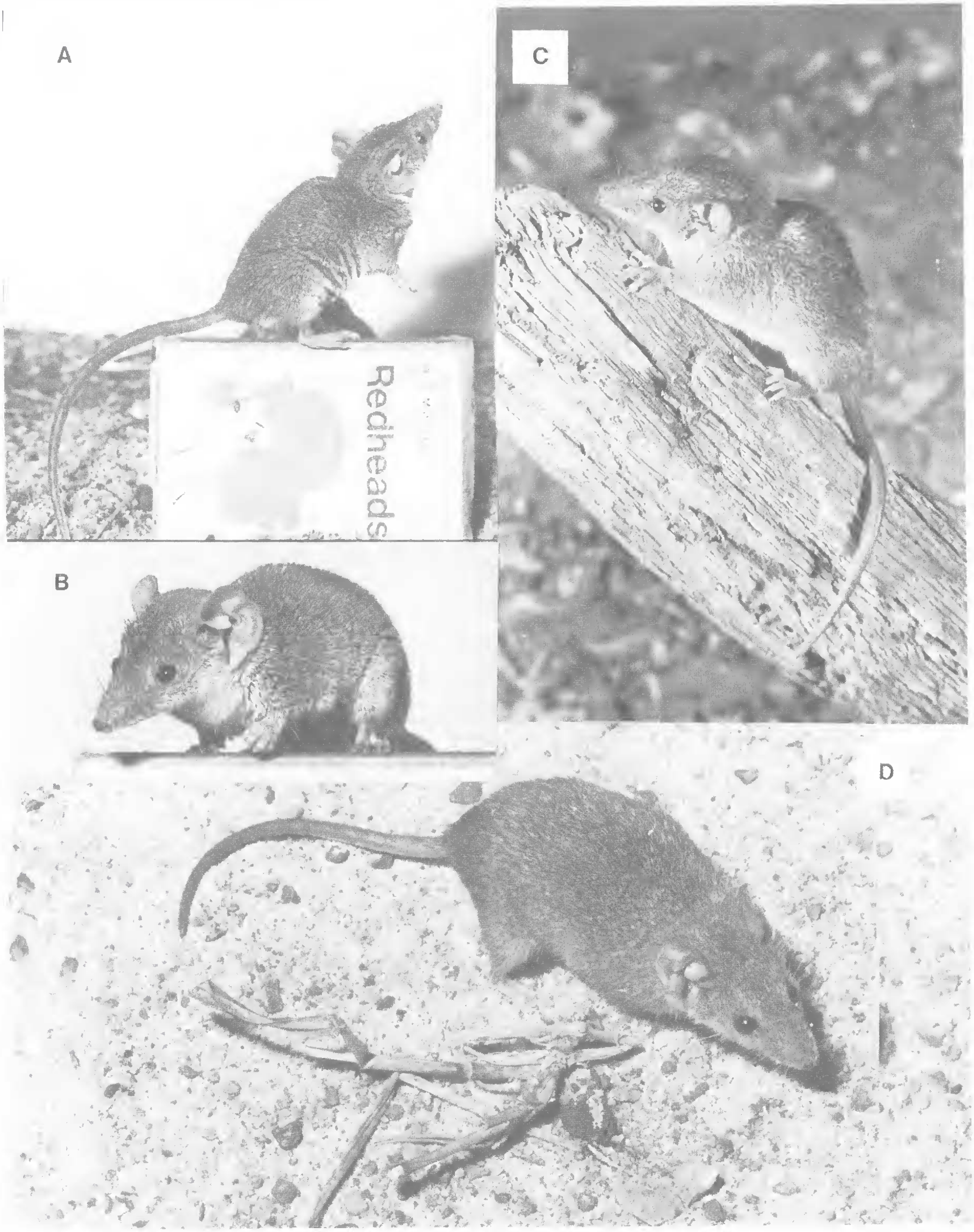
A–D, *Planigale* sp. WAM M3432, adult, Tambrey, W.A. A, × 5·6, B–D, × 4·0.



B
A
D
C

PLATE 51

A–B, *Planigale ingrami* (the *subtilissima* form), Ord River area, W.A. C–D, *Planigale maculata* (the typical form), Qd.


A
B
C
D
Redheads